University of Alberta

Response of environmental variable and understory vascular vegetation to various intensities of harvesting at the EMEND site, Northern Alberta

By

Treena E. Fenniak ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

In

Forest Biology and Management

Department of Renewable Resources

Edmonton, Alberta

Fall 2001

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Response of environmental variables and understory vascular vegetation to various intensities of harvesting at the EMEND site, Northern Alberta* submitted by *Treena E. Fenniak* in partial fulfillment of the requirements for the degree of Master of Science in Forest Biology and Management.

For Mom.

Thank you.

Abstract

Environmental variables and understory vascular vegetation were studied before
and after harvesting (clearcut, partial harvesting and control) within three forest
types in the boreal forest of Alberta. Results indicated that preharvest forest
communities, and stands within these communities, differed in amount of
downed wood and litter. The understory plant community in deciduous-
dominated forest was more diverse than those found in mixedwood and conifer
forests, and stand understory composition varied considerably within these
forest types. Soil temperature and moisture were the only environmental
variables correlated with harvesting in all forest types. Partial harvesting had less
effect on understory composition and diversity than clearcutting, especially in
the deciduous-dominated forest. Therefore, partial harvesting has potential as
an alternative to clearcutting that preserves natural composition. Results suggest
that forest managers should approach different forest types with different
methods.

Acknowledgement

I would like to thank my committee Dr. Stephen Titus and Dr. Vic Lieffers for their advice and assistance,

and especially my supervisor,

Dr. S. Ellen Macdonald,

whose tireless energy and generous help inspired me to do my best.

I would like to thank those who helped me in the field: Ed Stafford, Athena McKown, Erin Flynn, Kirstin Gregorwich and Charlene Hahn.

I would like to acknowledge the following organizations for their financial support:

C/BAR Grants from the Canadian Circumpolar Institute
Canadian Forest Products
Challenge Grants in Biodiversity
Daishowa – Marubeni International
Department of Renewable Resources

and

The Sustainable Forest Management Network

Last and dearest to my heart, I would like to thank my family and friends, especially

Adrienne and Arden Hill and Merle Elgert,

for their infinite patience and emotional support throughout this journey.

Table of Contents

List of Tables

Chapter 2

Chapter 3

List of Figures

Chapter 2

Chapter 3

Chapter 1: Introduction

Environment and its influence on understory vegetation

Based on extensive observation of existing boreal forest stands, there is an acknowledged difference of environment and plant community among forest types with different canopy composition (Rowe 1955). These seminal studies chronicle the differences among communities, and some postulated the aspen-mixedwood-conifer succession pathway based on these observations (Rowe 1955, Rowe 1961).

The differences among forest type environments are primarily related to the qualities of deciduous canopy compared to a coniferous canopy. The denser quality of a coniferous canopy increases light attenuation (Constabel and Lieffers 1996, Lieffers and Stadt 1994, Lieffers et al. 1999). This in turn lowers soil temperature, and may lower evaporation at the soil surface. In addition, the soils beneath a conifer canopy may experience an increase in acidity due to needle litter (Hausenbuiller 1985, Kimmins 1987). Mature deciduous canopies, with their less dense cover and seasonal loss of foliage, tend to allow more light and a different quality of light to penetrate. The seasonal leaf drop also contributes to a thick litter layer which affects ground level light (Schimpf and Danz 1999), and can also influence soil nutrients, temperature and moisture levels (Bird and Chatarpaul 1988, Cortina and Vallejo 1994).

Many studies of the boreal forest have also indicated relationships between canopy composition and understory species composition (Swan and Dix 1966, Purchase and La Roi 1982, Rowe 1955, Rowe 1961). For example, canopies containing conifer are commonly associated with proliferation of ground mosses such as *Hylocomium splendens* and *Pleurozium schreberi*, as well as certain shade tolerant shrubs and herbs, such as *Vaccinium spp*. (Dix and Swan 1971, Johnson et al.1995) but generally less understory plant cover and complexity of understory structure (Rowe 1955, DeGrandpre et al. 1993).

While these qualities have been clearly documented in each forest type, important questions remain unanswered. To what extent are the species related with a given forest type in Alberta's boreal forest a result of the environment

1

found in that forest? Rowe (1955) stated that a range of physiognomic factors affect vegetation of the boreal forest, including temperature, competition, litter and soil, but especially light. However, while that study and studies in other forest ecoregions suggest that there are correlations between environment and understory community, cause and effect relationships have not been determined. If environment does have a causative relationship with understory plant communities, it is important to determine if the relationships between environment and species composition are consistent across all forest types, or if different variables determine species composition in different forest types. This information could be invaluable to forest managers.

Succession in the boreal mixedwood

On mesic sites in the boreal forests of northern Alberta, succession is typically considered a singular path. Aspen dominated ecosystems are pioneer communities that precede the inevitable incursion of *Picea glauca* or other conifers, proceeding finally to coniferous-dominated communities (Rowe 1955, Rowe 1961, Dix and Swan 1971). More recent studies suggest that, while this pathway is common and even predominant, it is possible to find stands that have been dominated or codominated by *Populus tremuloides*, or other species considered early succession species, for as long as 200 years (Bergeron and Dubuc 1989, Cumming et al. 2000), well into the age range commonly classified as "old growth" (Bergeron and Dubuc 1989). The variables mentioned in all of these studies as paramount in determining the pathway of boreal succession, usually following fire, are seedbed and seed availability which regulate recruitment of canopy species (see also Lewin 1986, Hughes and Fahey 1991). These findings are consistent with the regeneration niche hypothesis proposed by Grubb (1977); his theory stated that a key step in development of a plant community was the point at which species have access to and establish on a disturbed site, other environmental factors may then further determine success of established seedlings and subsequent community development.

Grubb is just one of several ecological theorists who indicated that the establishment stage of succession is uniquely important. Grime (1977) suggested that at any given point in the succession process, plants grow in response to conditions resulting from a combination of environmental factors, including competition, stress and disturbance. Tilman (1985) further refined these ideas in his resource-ratio hypothesis, which posed two subhypotheses: "succession results from a gradient through time in the relative availabilities of limiting resources" and succession is only as repeatable or directional as the resource-supply trajectory. Therefore, while large-scale succession over the long term may be a repeating pattern, the progression of small-scale communities may vary considerably through time and space due to localized variations in environmental conditions.

Grubb's (1977) regeneration niche theory contains similar ideas focusing on the early stages of succession within the microsite environment. According to Grubb, a heterogeneous environment acting on every reproductive stage of plants can determine community species diversity. Put more simply, the microsite environment available following the death or removal of a plant can determine whether that plant will be replaced by another of its own or an individual of another species. Therefore, the removal of forest canopy and any associated changes in the environment could significantly influence the establishment of understory species. In addition, the type, frequency and/or severity of any disturbance, including harvesting could affect the postdisturbance species composition due to its effect on available niches. More recent studies, while highlighting the importance of Grubb's work, still maintain that the most important determinant of the presence/absence of a species is previous occupation of that site by the same species (Lewin 1986, Hughes and Fahey 1991).

Implications of differences among forest types for harvesting and forest managers

Roberts and Gilliam (1995) suggest that "comparative studies on different ecosystem types would provide insights into the relative importance of processes

that influence diversity". If certain forest types have unique relationships between environmental variables and understory plant communities, then diversity over the landscape may be a function of distribution of forest types as much as it is a function of species abundances. This may be likened to "process diversity" as described by Franklin (1998). If the assumption is made that all community-types are stages within a single pathway, then if shifts occur in the proportion of aspen to conifer on the landscape, it may not be considered a loss or shift in diversity. However, if the newer studies are right, and there is more than one successional pathway, changing the distribution of community types creates a different proportional representation of succession processes across the landscape, which may in turn alter distribution of associated understory species.

Forest managers may need to take different forest types into account if they hope to preserve the mosaic of landscape diversity, as currently recommended by many researchers (Kimmins 1997). This may be particularly important if forest types respond differently to different harvesting types. Is this likely?

Disturbance in the boreal forest

In the boreal forest of Alberta, disturbance by fire is the primary driving force of successional initiation (Carleton and Maycock 1980, Schaefer 1993). Many species specific to this region possess reproductive mechanisms that make them adapted to frequent burns. Some reproduce vegetatively from remnant underground organs, while others use heat-induced seed dispersal and/or germination (Foster 1985). Therefore, the species composition of existing mature forest stands within the boreal forest is primarily descended from a pioneer community adapted to a postfire environment.

The boreal forest is a rich source of wood fibre for the forest industry, and so harvesting has become an equally important source of disturbance in this region (Carleton and MacLellan 1994). Widespread industrial forestry is a relatively recent development in the history of Alberta's forests, and the primary method of timber removal to date is clearcutting, with a small amount of seed

4

tree or green patch retention. Changes in site condition following clearcutting have been well documented in eastern boreal forests, and in other forests in Canada (Keenan and Kimmins 1993, Carleton and MacLellan 1994, Foster 1985). Clearcutting can remove major portions of coarse woody material (CWM) and its associated nutrient pool (Foster 1985). Clearcutting may also disturb the litter and organic layer due to scraping, mixing and compaction; however, there is some evidence that there is little significant damage to the seedbank, just redistribution (Qi and Scarratt 1998). Due to the perturbation of the soil strata, as well as the removal of surface litter on harvested sites and reduced evapotranspiration, surface flow of water increases (Keenan and Kimmins 1993). The removal of live trees and destruction of structural elements such as snags and shading CWM on harvested sites decreases light attenuation and increases soil temperature as well. All of the above factors interact to provide a unique regenerative substrate in clearcut areas compared to that available immediately following natural disturbance or in an established boreal forest stand. If Grubb's regeneration niche theory holds true, the conditions found after clearcutting could precipitate a large-scale shift in species composition within the boreal forest away from that found following natural disturbance.

Natural Disturbance Paradigm

While it was not necessarily in recognition of the relationship between disturbance type and species composition in regenerating communities, forestry companies in Alberta's boreal forest have recently begun to adopt the natural disturbance paradigm as a model for sustainable forest management. In the western boreal forest, harvesting according to this paradigm aims to mimic the disturbance patterns caused by fire, the major source of natural disturbance in this region. By adopting this strategy, forestry companies hope to facilitate the growth of healthy postharvest communities within a landscape that closely resembles that found naturally. This appears to be even more pertinent in light of evidence that clearcut logging in Ontario's boreal forest has led to a significant change in the landscape distribution of forest community types (and therefore

associated plant communities) over the last 150 years (Spies et al. 1994, Jackson et al. 2000).

To manage forests in a sustainable fashion, and maintain regrowth of valuable timber, the natural disturbance paradigm promotes cutting in patterns reminiscent of postfire stands; one example is leaving patches of standing timber to simulate naturally occurring fire skips. However, simply copying fire patterns may not be sufficient to ensure that typical postfire species will return to the area. If harvesting can be performed in a way that will result in postdisturbance environmental conditions similar to those following natural disturbance that determine the regeneration niche of a site, it may be possible to produce a postdisturbance community more closely resembling that which may occur following natural disturbance.

While no suitable harvesting method has been found to date that emulates the conditions found following fire, there is another option. Namely, harvesting might be done in a way that does not return succession to the initial stages, but instead simply causes a small interruption in the ongoing process of natural succession. Therefore, forest managers need to find a method of harvesting that can yield sufficient timber and still lower the severity of disturbance to minimize restructuring of the forest mosaic.

Potential of partial harvesting

Narrow-strip partial harvesting is being proposed in this study as an alternative harvesting method that may provide a postdisturbance environment different from that found following clearcutting, and possibly of low enough impact that succession processes are not significantly altered. This would allow true natural disturbance to have persistent effects on succession instead of attempting to create an intense disturbance that is equivalent to fire. Studies of herb species distribution following partial canopy removal in deciduous forest indicate that with a loss of up to 66% of tree basal area, herb communities show no significant change in composition and distribution (Reader and Bricker 1992). Since partial canopy would be retained throughout the compartment, soil

temperatures and moisture could potentially remain relatively stable; although a rise in soil moisture has been observed with thinning in some forest types, there was an accompanying rise in transpiration rates (Bréda et al. 1995, Black et al. 1980). In addition, the restricted movement of harvesting equipment with partial cut harvesting could reduce compaction and soil mixing, as well as propagule damage. As with green-tree retention and patch-cutting partial harvesting techniques (North et al. 1996), it would be likely that there would be greater heterogeneity of microsite conditions than that following uniform clearcutting, possibly similar to the heterogeneous conditions found within mature, complex-structured forest stand. Even if light regimes are changed slightly by canopy removal, there may be enough shade to avoid extreme environmental changes and increased encroachment of competitive, early successional species (Reader and Bricker 1992, Lieffers et al. 1999).

The Ecological Management Emulating Natural Disturbance (EMEND) study site provided a unique opportunity to compare traditional and alternative harvesting methods, with strong temporal and spatial comparisons. The 14 km² site, containing 4 identified forest types (deciduous-dominated, mixedwood, conifer-dominated and aspen-dominated with conifer understory), included all of the presumed successional stages of the boreal mixedwood. In addition, a wide range of partial harvesting levels (10, 20, 50 and 75% levels of canopy retention) as well as clearcutting was applied within a single year, providing excellent opportunities for comparison of response.

This study aimed to discern whether microsite environments and understory vascular plant composition found following different strip harvesting intensities differ from those found following clearcutting or in a mature forest stand, and whether or not there is a relationship between changes in environmental variables and species composition changes within treatments.

Objectives

Within this thesis, I propose to:

7

Chapter 2

1. Characterize the environment found in mature deciduous-dominated, mixedwood and conifer-dominated boreal forest communities.

2. Characterize the understory vascular plant community composition and diversity in these forest types.

3. Determine which aspects (if any) of the environment might be important in determining understory plant community composition and/or diversity.

Chapter 3

1. Determine changes in the forest environment in the first two years following different levels of partial harvesting.

2. Determine changes in the understory vascular plant community during the period immediately following different levels of partial harvesting.

3. Elucidate any relationships between changes in the environment and changes in plant community composition following the different levels of harvesting.

4. Make some conclusions regarding the use of this type of partial harvesting by forest managers as a component of the "natural disturbance paradigm" approach to commercial harvesting.

Bibliography

Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the
Canadian boreal forest. Vegetatio 79: 51-63.

Bird, G.A. and L. Chatarpaul. 1988. Effect of forest harvest on decomposition and
colonization of maple leaf litter by soil microarthropods. Can. J. Soil Sci.
68: 29-40.

Black, T.A., C.S. Tan and J.U. Nnyamah. 1980. Transpiration rate in Douglas-fir
trees in thinned and unthinned stands. Can. J. Soil Sci. 60: 625-631.

Bréda, N., A. Granier and G. Aussenac. 1995. Effects of thinning on soil and tree
water relations transpiration and growth in an oak forest (Quercus
petraea (Matt.) Liebl.). Tree Physiol. 15: 295-306.

Carleton, T.J. and P. MacLellan. 1994. Woody vegetation responses to fire versus
clear-cutting logging: A comparative survey in the central Canadian
boreal forest. Ecoscience. 2: 141-152.

Carleton, T.J. and P.F. Maycock. 1980. Vegetation of the boreal forests south of
James Bay: Non-centered component analysis of the vascular flora.
Ecology. 61: 1199-1212.

Constabel, A.J. and V.J. Lieffers. 1996. Seasonal patterns of light transmission
through boreal mixedwood canopies. Can. J. For. Res. 26: 1008-1014.

Cortina J. and V.R. Vallejo. 1994. Efects of clearfelling on forest floor
accumulation and litter decomposition in a radiata pine plantation. For.
Ecol. Manag. 70: 299-310.

Cumming, S.G., F.K.A. Schmiegelow and P.J. Burton. 2000. Gap dynamics in
boreal aspen stands: is the forest older than we think? Ecol. Appl. 10: 744-
759.

DeGrandpré, L., D. Gagnon and Y. Bergeron. 1993. Changes in the understory of
Canadian southern boreal forest after fire. J. Veg. Sci. 4:803-801.

Dix, R.L. and J.M.A. Swan. 1971. The roles of disturbance and succession in
upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49: 657-676.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black
spruce) - *Pleurozium* forests of south-eastern Labrador, Canada. J. Ecol. 73:
517-534.

Franklin, S.F. 1998. Structural and functional diversity in temperate forests. In:
Wilson, EO (Ed.), *Biodiversity*. National Academy Press, Washington DC,
pp. 166-175.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration. Biol. Rev. 52: 107-145.

Hausenbuiller, R.L. 1985. Soil Science: Principles and Practices. Wm. C. Brown Publishers, Dubuque, Iowa. pp. 610.

Hughes, J.W. and T.J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J. Ecol. 79: 605-616.

Jackson, S.M., Pinto, F., Malcolm, J.R. and E.R. Wilson. 2000. A comparison of pre-European settlement (1857) and current (1981-1995) forest composition in central Ontario. Can. J. For. Res. 30: 605-612.

Johnson, D., L. Kershaw, A. MacKinnon and J. Pojar. 1995. Plants of the western boreal forest and aspen parkland. Lone Pine Press.

Keenan, R.J. and J.P. Kimmins. 1993. The ecological effects of clearcutting. Environ. Rev. 1: 121-144.

Kimmins, J.P. 1987. Forest Ecology. Macmillan: New York. 831 pp.

Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and integrity. Forestry Chronicle 73: 229-232.

Lewin, R. 1986. Supply-side ecology. Science 234: 25-27.

Lieffers, V.C., C. Messier, K.J. Stadt, F. Gendron and P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

North, M., Chen, Jiquan, Smith, G., Krakowiak, L. and J. Franklin. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Sci. 70: 24-35.

Purchase, J.E. and G.H. La Roi. 1982. *Pinus banksiana* forests of the Fort Vermillion area, northern Alberta. Can. J. Bot. 61: 804-824.

Qi, Meiqin and J.B. Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Can. J. Bot. 76: 872-883.

Reader, R.J. and B.D. Bricker. 1992. Value of selectively cut deciduous forest for understory herb conservation: An experimental assessment. For. Ecol. Manag. 51: 317-327.

Roberts, M.R. and F.S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecol. Appl. 5: 969-977.

Ross, M.S., L.B. Flanagan & G.H. LaRoi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Can. J. Bot. 64: 2792-2799

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Can. J. Bot. 39: 1007-1017.

Rowe, J.S . 1955. Uses of undergrowth plant species in forestry. Ecology. 37: 461-473.

Schaefer, J.A. 1993. Spatial patterns in taiga plant communities following fire. Can. J. Bot. 71: 1568-1573.

Schimpf, D. and N. Danz. 1999. Light passage through leaf litter: Variation among northern hardwood trees. Ag. For. Meteorology. 97: 103-111.

Spies, T.A., W.J. Ripple and G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4:555-568.

Swan, J.M.A. and R.L. Dix. 1966. The phytosociological structure of upland forest at Candle Lake, Saskatchewan. J. Ecol. 54: 13-40.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852.

Chapter 2: *Relationship between environmental variables and understory vascular vegetation under various canopy types at the EMEND site, Northern Alberta*[*]

Introduction

In the boreal forest, previous research has suggested that aspen dominated ecosystems are pioneer communities that precede the inevitable incursion of *Picea glauca* or other conifers, proceeding finally to coniferous-dominated communities (Rowe 1961, Dix and Swan 1971). More recent studies suggest that, while this pathway is common and even predominant, it is possible to find stands that have been dominated or codominated by *Populus tremuloides,* or other species considered early succession species, for as long as 200 years (Bergeron and Dubuc 1989, Cumming et al. 2000), well into the age range commonly classified as "old growth" (Bergeron and Dubuc 1989). The variables mentioned in all of these studies as paramount in determining the pathway of boreal succession, usually following fire, are seedbed and seed availability which regulate recruitment of canopy species (see also Lewin 1986, Hughes and Fahey 1991). The importance of the germination and establishment phase was a pivotal aspect of the regeneration niche hypothesis proposed by Grubb (1977); his theory stated that species must have access to and establish on a disturbed site before any other environmental factors may further determine success of seedlings, thus emphasizing the importance of this stage of succession.

Environmental conditions beneath different canopy types have been studied, and some fundamental environmental differences between coniferous, mixedwood and deciduous communities have been documented. The denser quality of conifer canopies increases light attenuation in comparison to a purely aspen canopy (Constabel and Lieffers 1996), and the acidic needle litter can lower soil pH. Deciduous canopies produce greater volumes of leaf litter because of seasonal loss, which can increase nitrogen content of the soil (Roberts et al. 1998). In addition, this seasonal leaf loss causes seasonal variation of light levels below

---

[*] Ed Stafford collected data in this chapter with the assistance of Athena McKown and Erin Flynn under the direction of Ellen Macdonald. Treena Fenniak did all subsequent analyses.

deciduous canopies. As a community that contains both of these species, mixedwood stands possess a blend of these characteristics.

Certain understory species have been commonly found associated with specific canopy composition; for example, canopies containing conifer are commonly associated with proliferation of ground mosses such as *Hylocomium splendens* and *Pleurozium schreberi*, as well as certain shade tolerant shrubs and herbs, such as *Vaccinium spp.* (Dix and Swan 1971, Johnson et al. 1995). In addition, spatial heterogeneity has been found to be highest in a mixedwood community (Shafi and Yarranton 1973), and this heterogeneity was presumed to create a more varied assortment of niches (*sensu* Grubb), which would provide opportunities for more species to establish. In addition, existing research suggested that mixedwood stands are the middle transitional stage of the successional process; the increased mortality of the pioneer species and increased success of the conifer species would create the most diverse set of niches within the temporal continuum, providing an opportunity for establishment of the largest number of species (Grubb 1977).

While common associations have been described between canopy and understory, studies need to address what processes are at work in creating these associations. This study assessed the canopy and understory composition and distribution of deciduous-dominated, mixedwood and conifer-dominated boreal forest stands, as well as the existing site-specific environmental conditions therein. These data were used to determine any relationships between environmental conditions and species composition that may elucidate the processes at work within particular canopy communities.

Management implications

Calls for maintenance of natural levels of biodiversity have been made by both researchers (Boyle 1991, Kimmins 1997, Hansen et al. 1991, Franklin 1993) and government agencies (Society of American Foresters 1991:viii). Regrettably, little consensus has been reached on when peak diversity occurs in succession (Roberts and Gilliam 1995) or even how to best quantify diversity (Kimmins

13

1997, Franklin 1993, Noss 1990). As early as 1961, research indicated that the boreal forests found in Alberta were best defined not by their climax state, since disturbance was frequent, but by their heterogeneity (Rowe 1961). These patterns of heterogeneity are found in forests at both the stand level and the landscape level (Kimmins 1997).

Ecosystem classifications according to canopy and understory vegetation and soil qualities have typically been used to classify forest stands prior to harvest; in the boreal forest of Alberta, stands are presumed to be stages within a set successional pathway based on these qualities (Beckingham and Archibald 1996). If the assumption is made that all aspen dominated stands are immature forests destined to become coniferous forests, then if shifts occur in the proportion of aspen to conifer on the landscape, it may not be considered a loss or shift in diversity. However, if the newer studies are right, and there is more than one successional pathway, changing the distribution of forest type creates a different proportional representation of successional processes across the landscape. Therefore, there may be implications in terms of preservation of diversity of natural process at the landscape level.

Objectives

In this study I propose to:

1. Characterize the environment found in deciduous-dominated, mixedwood and conifer-dominated boreal forest communities.

2. Characterize the understory vascular plant community composition and diversity in these forest types.

3. Determine which aspects (if any) of the environment might be important in determining understory plant community composition and/or diversity.

Methods

Site description

The EMEND (Ecological Management by Emulating Natural Disturbance) research project is located in the P2 forest management area (56

deg. 44 min. N, 118 deg. 20 min. W) of northern Alberta (Fig. 2-1). The EMEND project is a forest management experimental area established to evaluate and compare the impact of various harvesting treatments and natural disturbance on boreal forest communities. It is located in the Lower Boreal-Cordilleran Ecoregion, which has average summer temperatures of 12.8°C (July average of 15.1°C) and average precipitation of 464mm, two-thirds of which occurs in summer months (Strong and Leggat 1992). The study area is limited to mesic sites, which are typified by grey luvisolic soils and presence of *Populus tremuloides, Populus balsamifera, Picea glauca* and *Picea mariana* with smaller components of *Betula papyrifera* and *Pinus contorta*. The 14 km² study area consists of 10 upland stands divided into 100 - 10ha sample areas, hereafter referred to as compartments. Stands were classified according to canopy composition using Alberta Vegetation Inventory (AVI) maps (ground truthed the following year) and three replicate stands were selected of each canopy type (as defined below). Each stand was not necessarily a single, contiguous area, but may have consisted of proximal areas classified as the same according to AVI standards (see Appendix 5 for complete stand descriptions).

This study sampled only a portion of the EMEND site, including deciduous dominated (>75% deciduous canopy), conifer dominated (>75% conifer canopy) and mixedwood (co-dominant coniferous and deciduous, each 35-65%) community types. There were four or five 10 ha compartments within each of the three replicate stands of each forest type that were sampled, for a total of 39 compartments (Table 2-2).

Plot location

Plots were located semirandomly, using an existing baseline transect system. Baselines marked at 20m increments were established within each compartment by EMEND personnel (Fig. 2-2). Plots for this study were located in cardinal directions perpendicular to the baseline at random distances (selected from a random number table) off the baseline at a selected subset of the 20m increment markers (see Appendix 1 for plot locations). Increments were chosen

randomly with some constraints, including minimizing interference with other EMEND projects, and maintaining a minimum distance of 50m from compartment edges, landings or roads.

Eight plots were established per compartment. Overall, this study examined a total of 312 plots (Table 2-1). Plots were marked with 3 foot rebar (6 inches left exposed), which served as the plot center for a 3.99m radius tree plot (area = 50m²), and served as the base corner of the 2x2m shrub plot and its nested 1x1m herb plot (Fig. 2-2).

Understory vegetation sampling

Vegetation was sampled within the 2x2m shrub and 1x1m herb plots. Tree saplings less than 5m in height and all woody plants classified as shrubs by Johnson et al (1995) were assessed in the shrub plot. All of these species were assigned to a cover class within the shrub plot according to a 7-stage system (for all classification systems, see Appendix 2). Dwarf shrubs, forbs, grasses and sedges were all recorded in the herb plot according to these same cover classes. All vascular plants were identified to the species level, with the exception of several species that were too difficult to identify beyond genera in the field (for species list, see Appendix 3). These species (*Aster sp., Alnus sp., Lathyrus sp., Rosa sp.,* and *Salix sp.*) were identified only to the genus level. Cover classes for total lichen and total moss cover were also assigned in the herb plot.

Canopy vegetation sampling

The number of live trees (>5m in height) and standing dead trees (>2m in height) within a 3.99m radius were each counted and recorded by species, then converted to stems/ha. Basal area was also determined for each species using a BAF4 prism, then converted to m2/ha. Canopy percent cover was recorded at plot center using a convex spherical densiometer (average of four measures for each cardinal direction - N, S, E and W).

Environmental Variables

The environmental variables measured were selected on the basis of existing studies of forest environmental response to harvesting disturbance and which variables showed significant changes after harvesting in those studies (see Introduction).

Soil temperature was measured twice (once in July and once in August) using thermocouples (10 and 30 cm depths) permanently implanted at each tree plot center. Temperatures were corrected to minimize error due to fluctuating ambient temperature by averaging readings taken within a day and calculating the difference between each reading and the average. Moisture availability was measured at the same time as the temperature measurements, using an Environmental Sensors Inc. MP-97 time domain reflectometry system. All rounds of measurement were started a minimum of 24 hours following a major precipitation event. Moisture and temperature measurements were taken within a short period (4-5 days) to minimize variation due to time, and forest types and treatments were measured in random order to prevent confounding time-treatment or time-type interaction.

Resin bags were used to measure available nitrogen and phosphorus in the soil. Each nylon bag contained 45 mL of Amberlite IR-150 anion-cation exchange resin, and was soaked 3 times in 1M NaCl solution, rinsing in deionized water after each soaking. Bags were then repeatedly rinsed in deionized water until rinse water had a neutral pH, and refrigerated until buried. Bags were buried near the permanent plot marker at the earliest convenience after spring thaw, one per plot within the mineral soil at an approximate depth of 10cm. Collection occurred late in the summer, to maximize time in the ground. Resin was removed from the bag, mixed with 100 mL of 2M KCl, agitated on a bed shaker for 90 minutes, and then filtered. Extracts were analyzed using a Technicon Autoanalyzer to provide concentrations of available NO_3^-, NH_4^+ and $P-PO_4^{3+}$.

Decomposition rates were estimated using cellulose disks (Whatman #1 - 42.5 mm filter papers). Two disks were inserted into each nylon mesh bag and

buried near the permanent plot marker following spring thaw at the organic/mineral soil interface. Disks were removed from the site in late summer to maximize time in the ground, oven dried at 65°C for 24 hours and weighed. Weight loss over the burial period was used as the measure of decomposition rate.

The litter layer was identified as the part of the soil containing an identifiable intact component of litter materials. The organic layer was identified as any O or A horizons containing organic matter. Depths of both layers were measured at the base corner and opposite corner of each shrub plot.

Germination substrate was described in terms of percent cover of mineral soil, litter, moss and lichens within the herb plot and coarse woody material (CWM) percent cover in the shrub plot. Each piece of CWM in all shrub plots was counted and assessed according to a 7 stage decay class system (see Appendix 1 for all classification systems) and the diameter of each piece (>8cm) was measured at its widest point within the plot. All substrates were assigned a cover class within a 7 category cover class system.

Analyses

All conversions and proofing of data were done in Excel (Microsoft Corporation 2000). All cover class values were converted to the midpoint percent value of that cover class. Summary statistics were calculated for the species data including shrub, herb and total species richness and diversity (per plot and per compartment). Species diversity was calculated using the Shannon-Weiner (SW) index:

$$H'=\Sigma p_i * \ln p_i,$$

and the Simpson's index:

$$D= \Sigma (p_i^2),$$

where p is the proportional abundance of species i within the unit area, the SW index being more influenced by rare species, the Simpson's by dominant species.

All of the canopy structure and environmental variable data, as well as richness, Shannon-Weiner and Simpson's diversity indices for each plot and for each compartment (by combining the data from the eight plots) were analyzed using SAS software. To determine whether any of these variables differed among forest types or stands, each variable was analyzed separately using an ANOVA (PROC MIXED) analysis of fixed factors within a nested experimental design ($\alpha=0.05$) (Table 2-2). This analysis uses the Satterthwaite procedure to calculate approximate degrees of freedom, which provides appropriate least squared means and significance values for fixed factors in a mixed model (Littell et al. 1996). However, if the n value for the experimental design is small, results for random factors using PROC MIXED are not dependable. Thus, PROC GLM was used to test the significance of random variables.

Species data were preliminarily analyzed by correspondence analysis (CA) using CANOCO for Windows version 4.0 software (ter Braak 1987a), to determine whether there was segregation between forest types based on understory vegetation. After viewing the initial CA ordination, detrended CA (DCA) was used instead of CA, to reduce the 'arch effect'. This pattern is a product of a quadratic relationship between the axes that compresses and therefore disguises relationships within the ordination; detrending eliminates this confounding effect (ter Braak, 1987b). Per compartment abundance scores were used to construct the ordination, as per plot scores would make an ordination that was too crowded and difficult to interpret. The ordination was checked for groupings in relation to forest type.

Detrended canonical correspondence analysis (DCCA) was also used to analyze species composition, but this method uses environmental variables to construct the axes along which plot scores are graphed. Ordinations of plot scores were created to determine whether stands segregated within forest types. Ordinations of environmental variables were also plotted, to determine the relative contribution of each variable to the construction of each axis.

All of the canopy structure and environmental variables, excluding litter type (because it was only measured postharvest), were analyzed to determine

their relative importance in discriminating each forest type. Discriminant function analysis (DFA) was used to determine, in a stepwise format, which variables best explain the variance among forest types. This analysis was performed using SPSS version 10.0.5 software (SPSS Inc. 1999).

Results

Forest structure and environment

Canopy structure varied between forest types not on the basis of density or basal area, but instead by canopy cover (Fig 2-3). The deciduous community showed a significantly higher canopy cover than mixedwood or coniferous (Table 2-3 & Fig. 2-3). Snag density was lower in the deciduous dominated community, though not significantly (Table 2-3 and Fig. 2-3). All three forest types showed similar live tree densities, basal areas, heights and DBH.

Deciduous stands exhibited significantly higher soil temperatures at both 10 and 30 cm depths, lower soil moisture, lower CWM average diameter and cover per plot, and significantly thicker litter layer and higher litter cover (Table 2-3 & Fig. 2-3). No environmental variables were significantly different between mixedwood and coniferous forest types (Table 2-3). Only a few environmental variables show significant variance at the stand level, including live density, canopy height and mean DBH, as well as available NH_4^+ (Table 2-4).

Understory community richness and diversity

Combined cover values of understory plants were significantly higher in the lower canopy cover deciduous community (vs. mixed, $Pr>|t|$ =0.0496; vs. conifer, $Pr>|t|$ =0.0353), due largely to greater shrub cover (vs. mixed, $Pr>|t|$ =0.0221; vs. conifer, $Pr>|t|$ =0.0086) (Table 2-5). Richness, Shannon Weiner diversity and Simpson's diversity were calculated at both the plot and compartment level. With the exception of significantly higher shrub richness values in the deciduous community versus that in the conifer-dominated ($Pr>|t|$ =0.0382), compartment level comparisons suggested that all forest types had similar richness and diversity levels. However, there was a trend of higher

mean richness and Shannon-Weiner diversity under the deciduous canopy and lower under the coniferous canopy (Table 2-6). Richness and diversity per plot had more significant differences than per compartment measures. Per plot values of richness and Shannon-Weiner diversity were highest in the deciduous community and slightly lower in the mixedwood, but only the coniferous community was found to be significantly different from the deciduous (Table 2-5). The Simpson's diversity index did not indicate different patterns at different scales, showing no significant difference in per plot or per compartment values between forest types, with the exception of a higher per plot shrub index in the deciduous community than that in the coniferous community $(Pr > |t| = 0.0392)$.

Differences in richness and diversity were also found in the analysis of variance of the random factor stand (Table 2-7). Total understory richness $(Pr > F = 0.0047)$ and Shannon-Weiner diversity $(Pr > F = 0.0190)$ per plot were significantly different among stands, and there were significant differences in shrub richness $(Pr > F = 0.0010)$ and Shannon-Weiner diversity $(Pr > F = 0.0013)$. Simpson's herb and total diversity per compartment $(Pr > F = 0.0323; Pr > F = 0.0455)$ and per plot total diversity $(Pr > F = 0.0108)$ also showed significant variation among stands. Per compartment richness and Shannon-Weiner diversity values did not show significant variation at the stand level (Table 2-7).

Community composition

Understory composition differences among forest types were examined using species abundances per compartment in a detrended correspondence analysis (DCA) because ordination of all 312 plot scores was too difficult to interpret. Compartment level analysis may be more appropriate, as forestry-related field assessments of community response to any treatment are likely to be at a compartment level, not at a microsite level. Results indicated that while the deciduous community tended to be unique in its understory species composition, there was substantial overlap between the mixedwood and conifer communities (Fig. 2-4).

Many species were common to all forest types (see table of presence/absence in Appendix), but *Amelanchier alnifolia, Cornus stolonifera, Osmorhiza depauperata, Viola canadensis, Actaea rubra* and *Aralia nudicaulis* are among some of the species that characterize the understory of deciduous dominated stands (Fig. 2-5 – DCA of species scores). These species are described by Johnson et al. (1995) as preferring moist woods, thickets and/or clearings, with only *O. depauperata* reported as showing a preference for deciduous cover. Within the deciduous community, however, there was considerable variation in the species composition among stands (Fig. 2-6). Stand 1 had a greater abundance of *Rubus idaeus* and *Alnus spp.*, stand 2 has more *Rosa acicularis* and *Sheperdia canadensis* and stand 3 is segregated by *Symphorocarpus occidentalis* and saplings, including *Populus tremuloides* and *Picea glauca*.

Mixedwood and coniferous communities showed substantial overlap of plot scores indicating similar species composition, but ordination of each forest community indicated some segregation of stands within each forest type, which had already been hinted at by the ANOVA results (Table 2-7). Mixedwood stand 8 scores were separate in the ordination from those in stand 7 and 9, likely due to a greater abundance of shrub species, including *Rubus idaeus, Ribes spp.* and *Alder spp.* In the conifer dominated community, these same species were found more commonly in stand 4, segregating it from stands 5 and 6. Interestingly, the species that were found exclusively in coniferous and mixedwood communities were not commonly found in both, but in only one of these forest types (see presence/absence table in Appendix 4). For example, *Trientalis borealis, Ribes americanum*, and *Circaea alpina* were exclusive to coniferous stands, while *Sorbus scopulina, Pedicularis labradorica, Corallorhiza trifida* and *Dryopteris austriaca* were only found in mixedwood stands. Since these communities did not segregate, this would indicate that the unique species were found in too small an abundance to significantly affect composition. There were some species common to both the mixedwood and coniferous communities, but which were not found in the deciduous, including *Rubus acaulis, Equisetum scirpoides, Geocaulon lividum* and *Goodyeara repens*; all were found in very low abundances. *Moneses uniflora*

was also found exclusively in these communities, but since it is commonly confused with *Pyrola secunda,* which is ubiquitous, this was considered inconclusive.

Relationship between environmental variables and species distribution

Detrended canonical correspondence analysis (DCCA) of each forest type indicated that, within each forest type, some stands segregated themselves with regards to environmental variables, indicating that understory species distribution is site-specific, not strictly associated with canopy type (Fig. 2-6). Examining the environmental variables that characterize each forest type, a similar suite of variables separated each forest type *and* stands within forest types (Table 2-8 and Fig. 2-7). The stepwise selection of discriminating environmental variables (Table 2-8) indicated that 30cm depth soil temperature, litter depth and cover, snag density and organic layer depth (in that order) were primary determinants between forest types. However, DCCA of environmental variables within forest types indicated that shallow depth soil temperature, litter cover and/or depth plus CWM factors are the primary discriminating factors amongst stands within forest types as well (Fig. 2-7).

Discussion

Environment

There were differences in environment among forest types; however, only select environmental variables were significant. The only element of canopy structure that was significantly different was percent canopy cover, which was highest in the deciduous community, while conifer and mixedwood canopies had similar canopy cover. This is an indicator that light quantity and quality beneath a deciduous canopy were different than those beneath a mixedwood or conifer canopy, which has been substantiated in other studies (Constabel and Lieffers 1996). However, in this case, a higher percent cover was not indicative of lower quantity of light beneath the canopy.

The deciduous community had significantly higher soil temperature, lower CWM cover and diameter, and greater litter cover and depth than the other forest types, and differences in these variables between forest types are likely related to differences in canopy cover and composition. Deciduous canopies are known to allow more light through to the understory than conifer canopies, partly due to the thinner and 'trembling' quality of the deciduous foliage that allowed sunflecks, as well as the seasonal loss of cover due to leaf drop (Ross et al. 1986, Constabel and Lieffers 1996, Lieffers et al. 1999). This difference in light regime is reflected in the warmer temperatures found under the deciduous canopy. The large amounts of litter are likely a result of seasonal foliage loss, as well as the additional contribution of leaf litter by the extensive shrub layer. The greater CWM cover and diameter in the mixedwood and conifer communities were consistent with the assumption that conifer stands are later stages in succession; the higher snag densities of the conifer stands also support this assumption. Older stands are likely to have more signs of past tree mortality (Freedman 1993, Freedman et al. 1996).

Lack of significant difference in moisture levels may be explained partly by Henderson et al. (1977) who found no significant difference in throughfall in various forest types. Other factors affecting soil moisture levels, especially transpiration, would likely be affected by tree densities (Black et al. 1980, Bréda et al. 1995), which were similar in all forest types. Transpiration would also be affected by total leaf area; although deciduous forest had higher canopy cover, this is not a measure of total leaf area, and thus is not valid for estimating water vapour exchange area with any accuracy.

Understory composition

Understory plant communities were associated with specific forest types. However, while the mixedwood was predicted to be the most species diverse, this study found the deciduous community to be the most species rich and species diverse of the three types, with the highest amount of understory cover as well. The extensive shrub community associated with the deciduous

24

community was the likely cause for its relatively high cover, and the more complex light regime created by this more extensive shrub layer may have created a more heterogeneous environment for herbs (see next section).

The deciduous forest understory community, when assessed on the basis of compartment-level species abundances, was segregated from the mixedwood and coniferous communities, while there was little differentiation between the understory communities in the mixedwood and coniferous forest types. However, this segregation was not an indication that the species in the deciduous community were unique. In fact, there were few species that occurred solely in one forest type. *Amelanchier alnifolia, Cornus stolonifera, Osmorhiza depauperata, Viola canadensis, Aralia nudicaulis* and *Actaea rubra* were found only within the deciduous community. Interestingly, there were species found that were limited to only the mixedwood or the conifer communities, but the communities did not segregate in analysis. This does suggest that while there may be species unique to a given forest type, they may be in such small abundances that they do not contribute significantly to segregating the communities. In other words, the segregation of these communities may not be entirely because of a difference in which species were present, but may also be affected by differences in abundance of common plants.

Looking at plant composition at the plot level within each forest type, there was substantial variation in composition among plots, and stands tended to segregate within forest types. Since canopy cover and canopy composition varied little within each forest type, it can be assumed that these differences in understory species composition among stands were not driven solely by canopy structure (Qian et al. 1997, Pausas 1994).

Plant composition in relation to the environment

It is likely that the correlations found between plant species composition and environmental variables were not evidence of environmental factors determining what community established, but were instead artifacts of what canopy type was present (Purdy, B.G., S.E. Macdonald and M.R.T. Dale,

25

submitted to Silva Fennica). Leaf area index has been shown to be very consistent across stands with similar canopy type, regardless of other environmental factors such as soil type (Messier et al. 1998); therefore, while it may vary substantially among forest types, it tends to be uniform within those communities. Since abiotic variables (with the exception of available NH4+) also varied little within each forest type (Table 2-3), it can be surmised that the variation in abiotic factors between forest types may have been due to effects of existing canopy cover composition. It can also be assumed that the abiotic variables measured in this study were not important drivers of understory community composition. This was verified by the minimal contribution of these variables to constraining the axes in the DCCA.

Certain forest structure variables, such as CWM cover and litter cover, were strong segregating factors defining the three different forest types in the discriminant function analysis, but also as segregating factors among stands in the DCCAs. Since all of these environmental variables are a product of the plant community present in each stand, they serve less as drivers of stand composition, and more as a reflection of stand-level processes like self-thinning and seasonal leaf drop.

What then are the driving factors determining stand-level understory composition? One possibility is that edaphic factors that were not measured in this study, such as pH or clay/sand content, varied among the stands. Soils may have been slightly different among stands, providing a different post-disturbance regeneration niche during establishment for the understory plants, but still providing a hospitable substrate for the canopy species (Carleton and Maycock 1980). If this were the case, those species that were isolated to a specific stand type likely had a narrower niche than the canopy species, or a limited ability to propagate over long distances (Meier et al. 1995).

Differences in subcanopy light may also have been a controlling factor in understory composition. While the light penetrating the canopy may have been consistent throughout each forest type, a difference in the understory structure, especially a thick shrub layer, could have created a more complex effect on light

attenuation from stand to stand (Rowe 1955). This could have affected the light levels at the ground level, making them more spatially heterogeneous and creating a wider variety of niches for the herb species beneath the shrubs. There may be a relationship between the light and soil factors as well. Edaphic factors may influence which shrubs establish and/or succeed to form a shading layer (Messier et al. 1998) and the canopy may affect the success of those shrubs.

One other important determining factor in understory composition is the pool of species available postdisturbance to colonize a site. This is considered by some to be the single most important factor determining plant community composition (Hughes and Fahey 1991, Lewin 1986). All of these factors are consistent with the assumption that all of the plants in each compartment may establish at the same time, and any understory community that is associated with a given canopy is not a product of that canopy, but merely a co-establishing cohort (Carleton and Maycock 1980).

This does not eliminate light as a factor controlling community composition among forest types. Light must be considered as a factor controlling survival rather than establishment. The inherently higher levels of light found beneath a purely deciduous canopy provide an environment unique from that found under mixedwoods or coniferous canopies (Constabel and Lieffers 1996, Lieffers and Stadt 1994, Lieffers et al. 1999). In addition, mixedwood forests, though they contain deciduous trees, often experience below-canopy light levels similar that below a pure conifer forest due to the angle of incidence of light in northern forests (Constabel and Lieffers 1996). This might explain the segregation of communities among forest types. Once under- and overstory species establish in a stand based on the factors mentioned earlier in this section, and the canopy species overtop the understory, the shading effect of that canopy may cause certain species to flourish or recede in numbers.

Conclusions

The findings of this study lend themselves to argue that the three forest types studied here are not three separate communities. Instead, the stands within

each forest type are each positioned along a continuum, with deciduous dominated forest at one end, and conifer dominated at the other. This is strongly supported by the fact that those factors that define each forest type are also the factors that define stands.

Since forest communities do segregate themselves, it is likely that canopy and understory communities are related, but canopy composition is not the only driver of understory composition. The multilevel attenuation of light by the shrub layer and canopy as well as edaphic conditions are possible drivers, as is the presence of viable propagules. What species were on the site previously, and which ones get an opportunity to establish immediately following disturbance are extremely important determining factors in forest canopy and understory composition.

Management implications

Since forest types are different, replanting a forest of one canopy composition with seedlings of another tree species is going to affect future understory composition. A different canopy cover may affect the success of understory species beneath it. However, since the establishment of canopy and understory occur at the same time, there is no guarantee that the regrowth of the same canopy type on a given site is going to yield the same understory (Carleton and Maycock 1980). Other drivers, such as soil type and seed availability, may be more important at the establishment stage in assuring the return of a similar understory community (Hughes and Fahey 1991, Lewin 1986, Halpern 1988).

Since the majority of environmental factors that characterize each forest type and stand are biotic products of that forest, they serve more as indicators of stand process than as predictors of plant community composition. Therefore, they would serve little purpose as a tool for manipulating plant community recovery postdisturbance.

Based on this study, some predictions could be made regarding forest response to harvesting. Since some environmental variables are indicators of stand process, they will respond to any interruption of that process; however,

28

since they are not causative agents in determing plant community composition, they will not necessarily be correlated with any observed plant species patterns postharvest. In addition, since forest types are fundamentally different, they will respond differently to harvesting. Deciduous communities in particular would be likely to respond differently than a mixedwood or conifer community. Moreover, due to the greater richness and diversity of the deciduous community, it is possible that it may be a more resilient forest type, more able to tolerate harvesting disturbance (DeGrandpré and Bergeron 1997).

Forest types are fundamentally different, both in terms of environment and plant species composition. If forest managers and researchers hope to address the issue of harvesting in a sustainable fashion by using the natural disturbance paradigm, each forest type must be respected as a different system, and treated differently (DeGrandpré and Bergeron 1997).

Table 2-1. Distribution of plots used in this study within the EMEND site. Three stands were randomly selected within each forest type; four compartments were sampled within two of the stands, five compartments were sampled within the other stand. This was done to accommodate harvesting treatments (see Chapter 3).

Forest types	*Stands*	*Compartments per stand*	*Plots per compartment*	*Total # of plots*
3	2	4	8	192
3	1	5	8	120
			Total plots →	**312**

Table 2-2. Experimental design used in SAS statistical analysis examining differences in environment, canopy structure and species composition among the three forest types.

Variables	Error	Designation
Forest Type	Stand(Forest Type)	Fixed
Stand(Forest Type)	Compartment(Stand(Forest Type))	Random
Compartment(Stand(Forest Type))		Random
Plot(Stand (Forest Type))		random subsamples

Table 2-3. Results of ANOVA comparing forest structure and environment among forest types (fixed factor in SAS mixed model). Degrees of freedom (d.f.), F-values (F) and probability of Type 1 error (Pr>F) are given (Pr>F significant if <0.05), and d.f., t-values (t) and probability of Type 1 error (Pr>|t|) of between forest type comparisons of least squared means in SAS mixed model analysis (Pr>|t| significant if <0.05). Per plot values were used for all variables. Higher d.f. values for canopy cover, soil temperature, moisture and decomposition rate are due to using OLS estimation which sets negative estimated variance components to 0, causing the model to use the next level error term.

	d.f.	Forest Type		ddom - cdom		ddom - mix		cdom- mix	
		F	Pr>F	t	Pr>|t|	t	Pr>|t|	t	Pr>|t|
Canopy Structure									
Live density	5.93	0.00	0.9992	-0.01	0.9905	0.03	0.9792	0.04	0.9697
Snag density	5.92	2.13	0.2012	-2.01	0.0921	-0.59	0.5762	1.42	0.2071
Basal area	5.40	0.56	0.5989	-1.05	0.3394	-0.68	0.5258	0.37	0.7255
Canopy percent cover	36	10.54	0.0002	4.57	0.0001	2.70	0.0106	-1.87	0.0696
Canopy height	5.97	0.45	0.6602	-0.90	0.4033	-0.70	0.5111	0.20	0.8465
Mean DBH	5.88	0.20	0.8211	-0.59	0.5767	-0.51	0.6317	0.09	0.9342
Environmental Variables									
Soil Temperature (10cm)	35	22.66	0.0001	6.09	0.0001	5.48	0.0001	-0.72	0.4738
Soil Temperature (30cm)	35	26.08	0.0001	6.59	0.0001	5.81	0.0001	-0.89	0.3795
Soil percent moisture	35	1.56	0.2250	-1.72	0.0951	-1.20	0.2379	0.54	0.5933
CWM									
# of pieces	6.43	0.21	0.8171	-0.64	0.5414	-0.35	0.7351	0.29	0.7800
Average diameter	6.31	0.89	0.4574	-1.10	0.3103	-1.20	0.2737	-0.10	0.9265
Total cover	6.33	1.25	0.3499	-1.55	0.1687	-1.02	0.3467	0.54	0.6094
Available NO_3^-	5.52	0.57	0.5957	0.11	0.9201	-0.87	0.4215	-0.97	0.3711
Available NH_4^+	5.72	0.13	0.8831	-0.18	0.8599	-0.50	0.6367	-0.31	0.7645
Available PO_4^{3+}	6.47	0.93	0.4403	1.37	0.2193	0.70	0.5089	-0.68	0.5190
Litter layer depth	5.77	10.74	0.0114	4.58	0.0042	2.91	0.0281	-1.66	0.1494
Organic layer depth	6.23	2.22	0.1871	-2.11	0.0782	-1.13	0.2992	0.97	0.3669
Decomposition rate	302	0.51	0.5996	0.45	0.6504	1.01	0.3131	0.56	0.5773
Litter cover	5.91	6.36	0.0335	2.86	0.0292	3.27	0.0173	0.41	0.6955

Table 2-4. Results of general linear model analysis of canopy structure and environmental variables F-values (F) and probability of Type 1 error (Pr>F) of random factors stand and compartment (Pr>F significant if <0.05) are given.

	Stand nested within type numerator d.f.= 6 denominator d.f. = 30		Compartment nested within stand numerator d.f. = 30 denominator d.f. = 273	
	F	Pr>F	F	Pr>F
Canopy Structure				
Live density	7.016	*0.0001*	4.181	*0.0001*
Snag density	2.300	0.0600	2.938	*0.0001*
Basal area	1.374	0.2570	1.910	*0.0039*
Canopy percent cover	0.225	0.9650	2.214	*0.0005*
Canopy height	5.754	*0.0004*	1.120	0.3100
Mean DBH	4.918	*0.0010*	1.936	*0.0033*
Environmental Variables				
Soil Temperature (10cm)	0.905	0.5040	11.140	*0.0001*
Soil Temperature (30cm)	0.918	0.4960	13.660	*0.0001*
Soil percent moisture	0.673	0.6720	5.095	*0.0001*
CWM				
# of pieces	1.360	0.2630	2.765	*0.0001*
Average diameter	1.521	0.2050	2.402	*0.0001*
Total cover	0.985	0.4530	3.377	*0.0001*
Available NO_3^-	1.512	0.1900	3.005	*0.0001*
Available NH_4^+	4.026	*0.0050*	1.788	*0.0088*
Available PO_4^{3+}	1.103	0.3840	3.160	*0.0001*
Litter layer depth	2.317	0.0590	9.138	*0.0001*
Organic layer depth	2.332	0.0570	3.829	*0.0001*
Decomposition rate	0.456	0.8350	0.577	0.9643
Litter cover	0.791	0.5850	1.036	0.4193

Table 2-5. Results of ANOVA comparing understory plant community diversity indices among forest types (fixed factor in SAS mixed model). Degrees of freedom (d.f.), F-values (F) and probability of Type 1 error (Pr>F) are given (Pr>F) significant if <0.05). D.F., t-values (t) and probability of Type 1 error (Pr>|t|) of between forest type comparisons of least squared means (Pr>|t|) significant if <0.05) of plant community variables are also given.

	Forest Type			ddom - cdom		ddom - mix		cdom - mix	
	d.f.	F	Pr>F	t	Pr>|t|	t	Pr>|t|	t	Pr>|t|
Percent cover/plot									
Herb	5.76	0.79	0.4979	0.88	0.4158	1.22	0.2709	-0.34	0.7452
Shrub	5.54	8.79	0.0191	3.97	0.0086	3.15	0.0221	0.83	0.4434
Combined	5.81	4.54	0.0649	2.73	0.0353	2.47	0.0496	0.26	0.8059
Richness/plot									
Herb	6.13	3.99	0.0776	2.76	0.0320	1.90	0.1058	0.87	0.4187
Shrub	5.91	3.60	0.0951	2.60	0.0415	1.88	0.1095	0.71	0.5030
Combined	6.00	4.63	0.0609	2.96	0.0252	2.08	0.0827	0.88	0.4117
Shannon-Weiner Diversity/plot									
Herb	6.04	3.36	0.0921	2.61	0.0399	1.89	0.1077	0.72	0.4970
Shrub	5.96	3.39	0.1038	2.54	0.0446	1.79	0.1246	0.75	0.4824
Combined	6.00	1.12	0.3857	1.49	0.1861	0.85	0.4290	0.64	0.5429
Simpson's Diversity/plot									
Herb	5.83	1.70	0.2623	-1.84	0.1175	-1.06	0.3315	-0.78	0.4676
Shrub	6.36	3.44	0.0970	-2.59	0.0392	-0.92	0.3923	-1.67	0.1430
Combined	5.96	0.47	0.6461	-0.90	0.4010	-0.15	0.8872	-0.76	0.4783
Richness/compartment									
Herb	6.10	1.12	0.3846	1.50	0.1840	0.75	0.4828	-0.75	0.4806
Shrub	5.98	3.97	0.0800	2.65	0.0382	2.16	0.0747	-0.49	0.6399
Combined	6.12	2.10	0.2027	2.02	0.0893	1.31	0.2368	-0.71	0.5062
Shannon-Weiner Diversity/compartment									
Herb	6.02	0.90	0.4560	1.34	0.2288	0.69	0.5144	-0.65	0.5416
Shrub	6.01	0.79	0.4972	1.13	0.3015	1.04	0.3398	-0.09	0.9286
Combined	5.90	0.18	0.8403	0.25	0.8086	-0.34	0.7435	-0.60	0.5731
Simpson's Diversity/compartment									
Herb	6.03	0.26	0.7793	-0.71	0.5025	-0.26	0.8011	0.45	0.6686
Shrub	5.82	0.82	0.4847	-1.28	0.2498	-0.73	0.4942	0.55	0.6035
Combined	5.93	0.27	0.7748	-0.04	0.9686	0.61	0.5641	0.65	0.5390

Table 2-6. Understory plant community indices per plot and per compartment (means and standard errors). Different letters indicate significantly different values among forest types based on results of least squared means comparison (p<0.05)

	ddom		mixed		cdom	
	mean	s.e.	mean	s.e.	mean	s.e.
Richness/plot						
Herb	10.48^a	0.30	9.02^{ab}	0.28	8.33^b	0.28
Shrub	3.36^a	0.12	2.47^{ab}	0.13	2.11^b	0.12
Combined	13.84^a	0.32	11.49^{ab}	0.34	10.43^b	0.33
Percent cover/plot						
Herb	48.88	3.12	37.80	2.40	40.76	2.85
Shrub	48.49^a	3.26	21.44^b	2.48	14.44^b	1.72
Combined	97.37^a	3.68	59.25^b	3.88	55.21^b	3.53
Shannon-Weiner Diversity/plot						
Herb	1.69^a	0.04	1.52^{ab}	0.04	1.46^b	0.04
Shrub	0.80^a	0.03	0.56^{ab}	0.04	0.44^b	0.04
Combined	1.83	0.04	1,74	0.04	1.66	0.04
Simpson's Diversity/plot						
Herb	0.28	0.01	0.31	0.01	0.34	0.02
Shrub	0.54^a	0.02	0.59^{ab}	0.03	0.67^b	0.03
Combined	0.25	0.01	0.25	0.01	0.28	0.01
Richness/compartment						
Herb	23.38	0.54	22.23	0.99	21.15	0.67
Shrub	7.69^a	0.38	6.08^{ab}	0.50	5.69^b	0.47
Combined	31.08	0.75	28.31	1.37	26.85	1.02
Shannon-Weiner Diversity/compartment						
Herb	2.34	0.09	2.25	0.05	2.16	0.07
Shrub	1.32	0.04	1.18	0.08	1.16	0.09
Combined	2.47	0.09	2.52	0.04	2.45	0.06
Simpson's Diversity/compartment						
Herb	0.16	0.03	0.17	0.01	0.19	0.02
Shrub	0.33	0.01	0.37	0.03	0.40	0.04
Combined	0.14	0.02	0.12	0.01	0.13	0.01

Table 2-7. Results of SAS general linear model analysis of per plot and per compartment plant community measures. F-values (F) and probability of Type 1 error (Pr>F) of random factors stand and compartment in SAS (Pr>F significant if <0.05) are given.

	Stand nested within type numerator d.f.=6 denominator d.f. = 30		Compartment nested within stand numerator d.f. = 30 denominator d.f. = 273	
	F	Pr>F	F	Pr>F
Percent cover/plot				
Herb	2.0952	0.0834	3.3314	*0.0001*
Shrub	1.6781	0.1608	5.1225	*0.0001*
Combined	2.8449	*0.0259*	4.6974	*0.0001*
Richness/plot				
Herb	1.9602	0.1032	2.2001	*0.0005*
Shrub	5.0936	*0.0010*	1.6359	*0.0228*
Combined	3.9884	*0.0047*	1.8083	*0.0077*
Shannon-Weiner Diversity/plot				
Herb	1.6689	0.1631	1.7677	*0.0100*
Shrub	4.9319	*0.0013*	1.4304	0.0736
Combined	3.0477	*0.0190*	1.6720	*0.0183*
Simpson's Diversity/plot				
Herb	1.9719	0.1013	1.5175	*0.0456*
Shrub	1.3603	0.2624	1.4233	0.0765
Combined	3.4186	*0.0108*	1.3872	0.0924
Richness/compartment				
Herb	2.2694	0.0634	-	-
Shrub	1.4437	0.2312	-	-
Combined	2.1810	0.0729	-	-
Shannon-Weiner Diversity/compartment				
Herb	2.2879	0.0616	-	-
Shrub	1.9946	0.0978	-	-
Combined	1.9029	0.1130	-	-
Simpson's Diversity/compartment				
Herb	2.6998	*0.0323*	-	-
Shrub	1.7060	0.1539	-	-
Combined	2.4807	*0.0455*	-	-

Table 2-8. Results of stepwise discriminant function analysis of environmental variables used to classify forest types. Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions. Variables ordered by absolute size of correlation within function – larger values indicate greater importance of variable in classifying forest types. Largest absolute correlation between each variable and any discriminant function indicated by italics. [a] These variables not used in the stepwise analysis.

Environmental Variables	Axis 1	Axis 2
Soil temperature - 30cm	*0.623*	0.404
Soil temperature - 10cm[a]	*0.538*	0.350
Litter depth	*0.537*	-0.472
Litter cover	*0.462*	0.246
CWM - # of pieces[a]	*-0.094*	-0.078
PO_4^{3+} [a]	*0.076*	0.034
Snag density	-0.158	*0.529*
Organic layer depth	-0.182	*0.275*
DBH[a]	0.007	*-0.187*
Canopy cover[a]	0.165	*0.177*
CWM - average diameter[a]	0.021	*-0.139*
CWM - total cover[a]	-0.068	*-0.136*
Canopy height[a]	-0.040	*-0.132*
Soil moisture[a]	0.024	*0.119*
NH_4^+	-0.031	*-0.104*
Basal area[a]	0.030	*0.082*
Live tree density[a]	-0.013	*0.082*
CWM - average decay class[a]	0.030	*-0.067*
NO_3^- [a]	0.031	*0.040*
Decomposition rate[a]	-0.019	*-0.035*
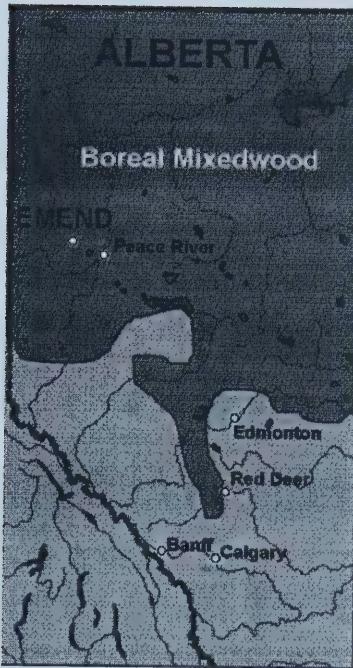
Fig. 2-1 – Location of EMEND study site
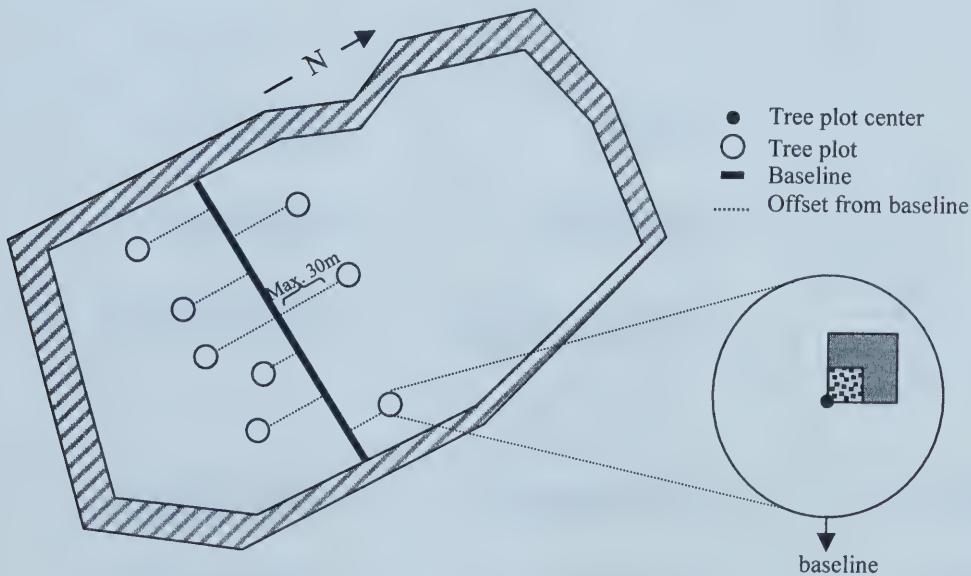
Figure 2-2. Layout of plots within each compartment (not to scale). Plots were offset from the existing baseline at distances selected from a random number table (<30 m). Magnified section shows a 1X1m herb plot (speckle) nested within a 2X2m shrub plot (gray) within a 50m^2 circular tree plot. The striped area is a buffer (minimum 100m wide).
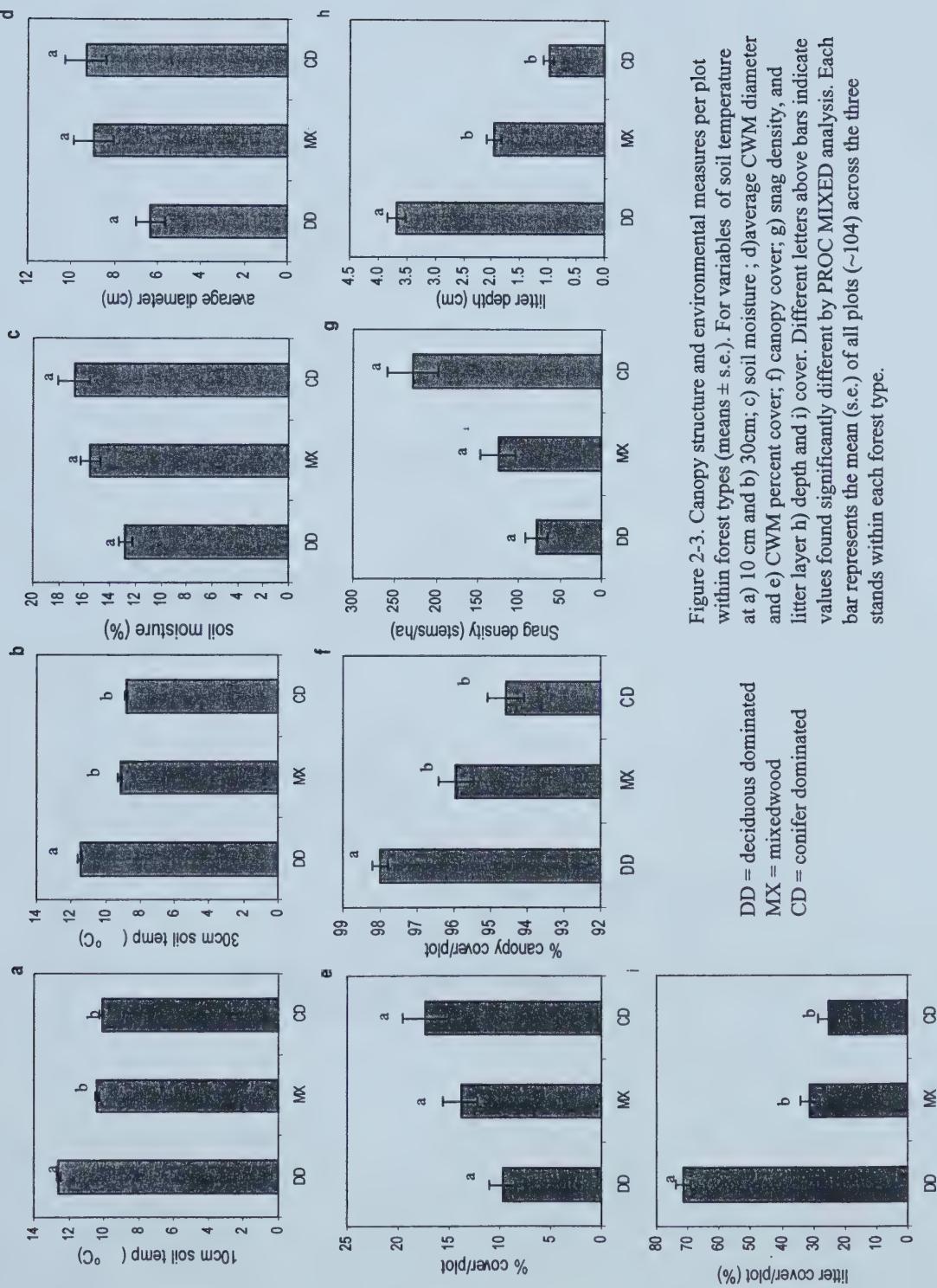
Figure 2-3. Canopy structure and environmental measures per plot within forest types (means ± s.e.). For variables of soil temperature at a) 10 cm and b) 30cm; c) soil moisture ; d)average CWM diameter and e) CWM percent cover; f) canopy cover; g) snag density, and litter layer h) depth and i) cover. Different letters above bars indicate values found significantly different by PROC MIXED analysis. Each bar represents the mean (s.e.) of all plots (~104) across the three stands within each forest type.

DD = deciduous dominated
MX = mixedwood
CD = conifer dominated

38

Figure 2-4. DCA of compartment scores based on understory species composition of all forest types (d = deciduous dominated, c = conifer dominated, m = mixedwood).
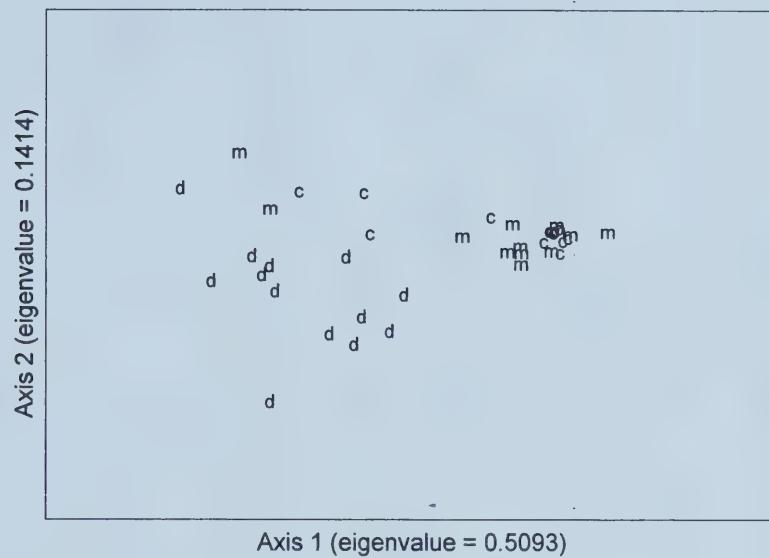
Figure 2-5. DCA of species scores based on per compartment abundances (lowercase = herb plot species, uppercase = shrub plot species; for abbreviations, see species list in Appendix 3).
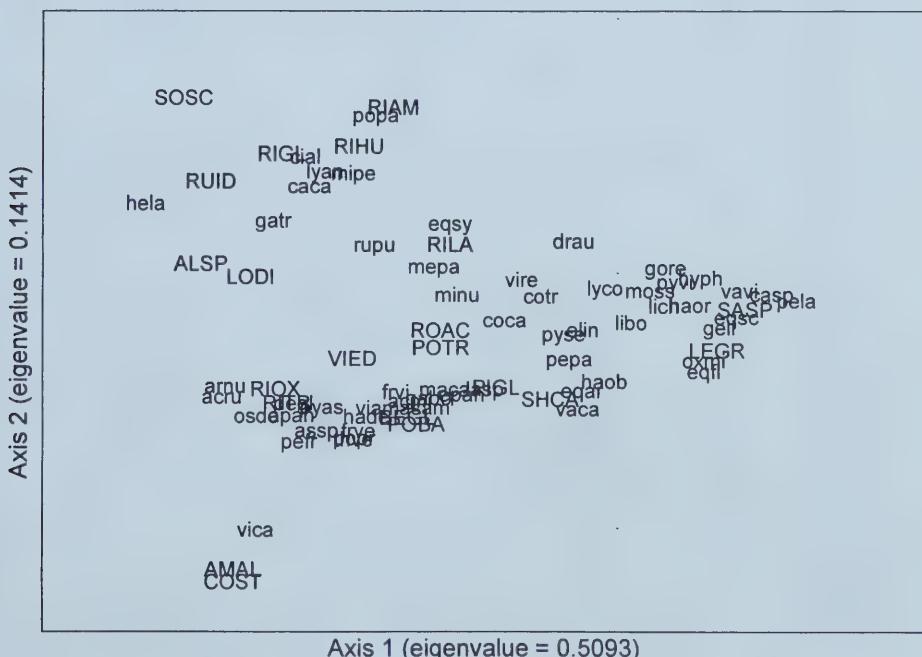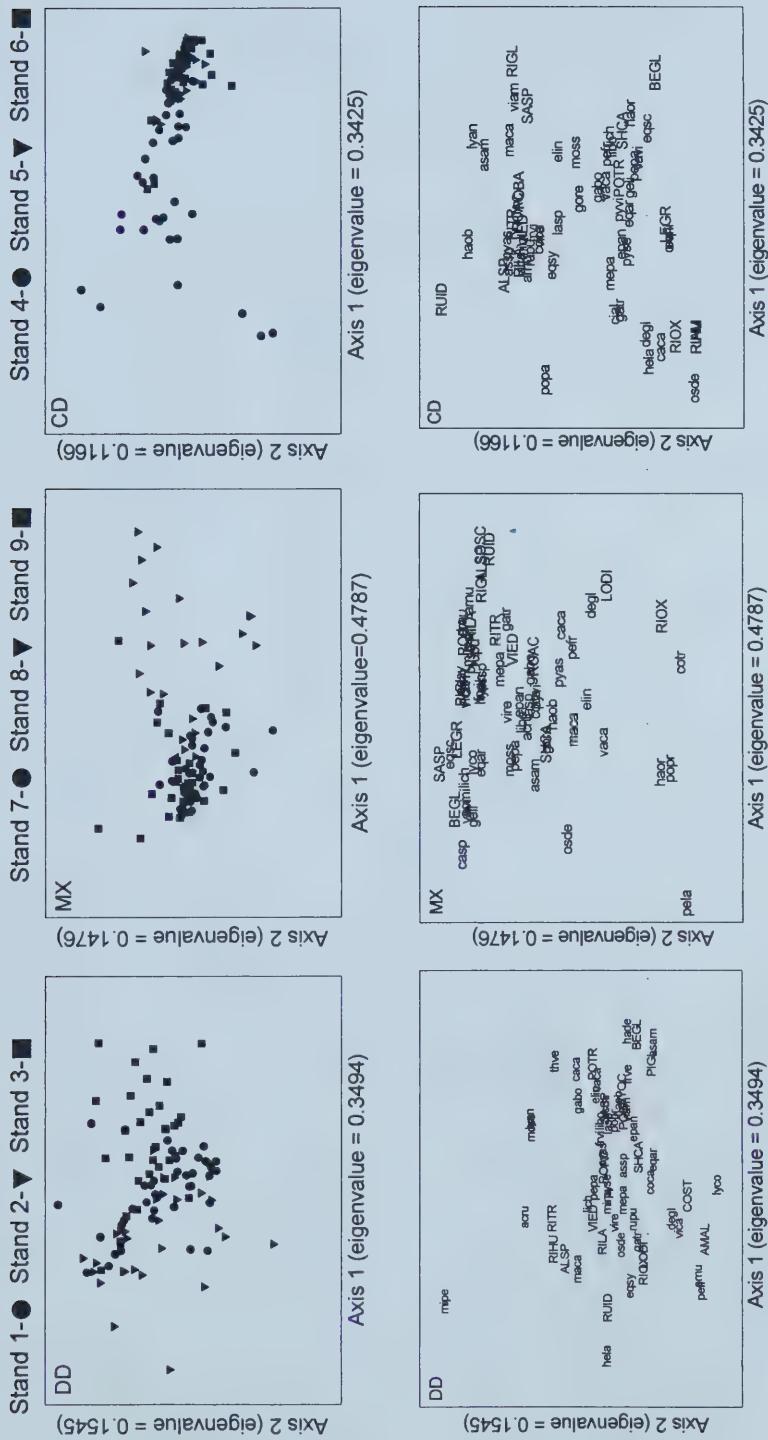
Figure 2-6. Distribution of DCCA plot and species scores for each forest type. Symbols represent plots within stands as indicated for deciduous-dominated (DD), mixedwood (MX) and coniferous-dominated (CD) forest types (see species list in Appendix for abbreviations).

40
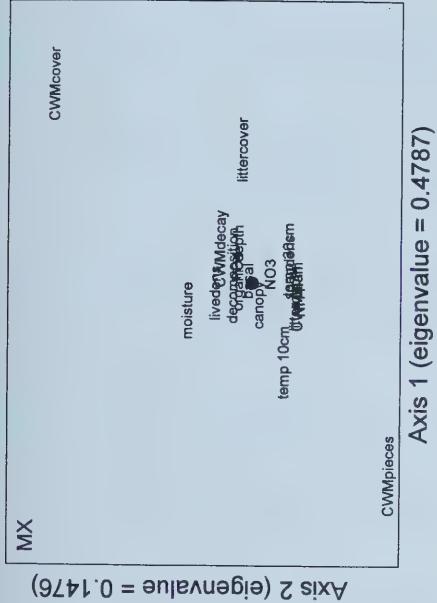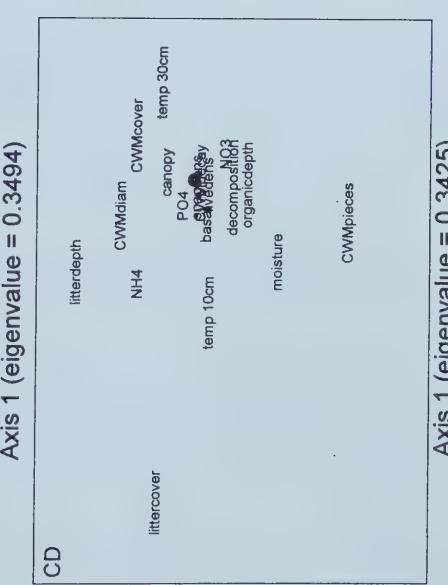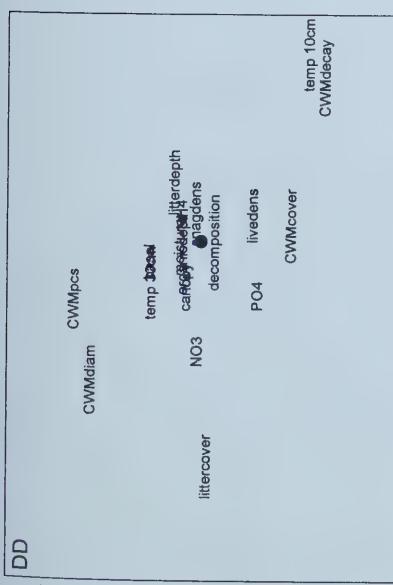
Figure 2-7. Distribution of DCCA environmental variable scores within deciduous-dominated (DD), mixedwood (MX) and coniferous-dominated (CD) forest types with relation to zero correlation point (• = coordinate 0,0). Those variables farthest away from • are proportionally the most important discriminants in plot distribution.

41

Bibliography

Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79: 51-63.

Black, T.A., C.S. Tan & J.U. Nnyamah. 1980. Transpiration rate in Douglas-fir trees in thinned and unthinned stands. Can. J. Soil Sci. 60: 625-631.

Boyle, T.J.B. 1991. Biodiversity of Canadian forests: Current status and future challenges. Forestry Chronicle 68: 444-452.

Bréda, N., A. Granier & G. Aussenac. 1995. Effects of thinning on soil and tree water relations transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol. 15: 295-306.

Carleton, T.J. & P.F. Maycock. 1980. Vegetation of the boreal forests south of James Bay: Non-centered component analysis of the vascular flora. Ecology 61: 1199-1212.

Constabel, A.J. & V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26: 1008-1014.

Cumming, S.G., F.K.A. Schmiegelow and P.J. Burton. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. 10: 744-759.

DeGrandpré, Louis & Yves Bergeron. 1997. Diversity and stability of understory communities following disturbance in the southern boreal forest. J. Ecol. 85:77-784.

Dix, R.L. and J.M.A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49: 657-676.

Franklin, J.F. 1993. Preserving biodiversity: Species, ecosystems or landscapes? Ecol. Appl. 3: 202-205.

Freedman, B. 1993. Old-growth forests and ecologically sustainable forestry. *In* Forestry on the hill. Old growth forests. Canadian Forestry Association, Ottawa, Ont. pp. 29-32.

Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, J.S. Gerrow, G. Johnson & S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4: 238-265.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52: 107-145.

Halpern, Charles. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69: 1703-1715.

Hansen, A.J., T.A. Spies, F.J. Swanson and J.L. Ohmann. 1991. Conserving biodiversity in managed forests. Bioscience 41: 382-392.

Henderson, G.S., W.F. Harris, D.E. Todd, Jr. and T. Grizzard. 1977. Quantity and chemistry of throughfall as influenced by forest type and season. J. Ecol. 65: 365-374.

Hughes, J.W. and T.J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J. Ecol. 79: 605-616.

Johnson, D., L. Kershaw, A. MacKinnon & J. Pojar. 1995. Plants of the western boreal forest and aspen parkland. Lone Pine Press.

Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and integrity. Forestry Chronicle 73: 229-232.

Lewin, R. 1986. Supply-side ecology. Science 234: 25-27.

Lieffers, V.J. and K. Stadt. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis* and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24: 1193-1198.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron & P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

Littell, R.C., G.A. Milliken, W.W. Stroup and R.D. Wolfinger. 1996. SAS System for Mixed Models. Cary, NC: SAS Institute Inc., 633 pp.

Meier, A.J., Susan Power Bratton & D.C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecol. Appl. 5: 935-946.

Messier, C., S. Parent and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9: 511-520.

Noss, R.F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. Cons. Biol. 4: 355-364.

Pausas, J.G. 1994. Species richness patterns in the understory of Pyrenean *Pinus sylvestris* forest. J. Veg. Sci. 5: 517-524.

Qian, Hong, Karel Klinka & Bela Sivak. 1997. Diversity of the understory vascular vegetation in 40 year-old and old-growth forest stands on Vancouver Island, British Columbia. J. Veg. Sci. 8: 773-780.

Roberts, B.A., K.W. Deering & B.D. Titus. 1998. Effects of intensive harvesting on forest floor properties in *Betula papyrifera* stands in Newfoundland. J. Veg. Sci. 9: 521-528.

Roberts, M.R. and F.S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecol. Appl. 5: 969-977.

Ross, M.S., L.B. Flanagan & George H. LaRoi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Can. J. Bot. 64: 2792-2799.

Rowe, J.S. 1955. Uses of undergrowth plant species in forestry. Ecology. 37: 461-473.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Can. J. Bot. 39: 1007-1017.

Shafi, M.I. and G.A. Yarranton. 1973. Vegetational heterogeneity during a secondary postfire succession. Can. J. Bot. 51: 73-90.

Society of American Foresters. 1991. Biological diversity in forest ecosystems. SAF Publication 91-03. Society of American Foresters, Bethesda, Maryland, USA.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Land Information Services Division. Edmonton, Alberta, Canada.

ter Braak, C.J.F. 1987a. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. TNO Institute of Applied Computer Science. Wageningen.

ter Braak, C.J.F. 1987b. 5. Ordination. In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.) Data analysis in community and landscape ecology, pp. 91-173. Pudoc, Wageningen.

Chapter 3: *Response of environmental variables and understory vascular vegetation to various intensities of harvesting at the EMEND site, Northern Alberta*

Introduction

Beginning from a disturbed state, a site is initially colonized by pioneer species. Competitive interactions as well as stress tolerance and mortality then may lead to changes in composition over time (Connell and Slatyer 1977). In addition, other species may colonize, producing further changes in community composition. Which species establish on the site depends on many factors, including site conditions, availability of reproductive propagules and the composition of the predisturbance community. Thus, a plant's life history and resource use strategy are important in determining its role in successional development (Grime 1977). Disturbance type plays an important role in succession, as it is the starting point of the process. The site conditions provided by a given disturbance help to determine which plants can establish, which may in turn exert an influence on the course and rate of later vegetational development (Foster 1985).

After disturbance, initial regrowth of vegetation occurs as a function of production of viable seed or other reproductive organs, dispersal of these in space and time, and successful germination (Grubb 1977). The specific substrate available on a given site drives plant establishment and growth through individual species responses to environmental conditions. Grime (1977) suggested that at any given point in the succession process, plants grow in response to conditions resulting from a combination of environmental factors, including competition, stress and disturbance. Tilman (1985) further refined these ideas in his resource-ratio hypothesis, which posed two subhypotheses: "succession results from a gradient through time in the relative availabilities of limiting resources"; and succession is only as repeatable or directional as the resource-supply trajectory. Therefore, while large scale succession over the long term may be a repeating pattern, the progression of small scale communities may

45

vary considerably through time and space due to localized variations in environmental conditions.

Grubb's (1977) regeneration niche theory contains similar ideas focusing on the early stages of succession within the microsite environment. According to Grubb, a heterogeneous environment acting on every reproductive stage of plants can determine community species diversity. Put more simply, the microsite environment available following the death or removal of a plant can determine whether that plant will be replaced by another of its own or an individual of another species. Therefore, the removal of forest canopy and any associated changes in the environment could significantly influence the establishment of understory species. More recent studies, while highlighting the importance of Grubb's work, still maintain that the most important determinant of the presence/absence of a species is previous occupation of that site by the same species (Lewin 1986, Hughes and Fahey 1991).

Research by Landhausser and Lieffers (1997) suggests that the regeneration niche could be extremely influential in succession, since early establishment may be more important than competitive ability in determining future successional development. Since understory species establish at the beginning of succession (Black and Bliss 1978), and their presence can be strongly linked to subsequent forest composition (Shaefer 1993), studying early postdisturbance conditions and understory regrowth and biodiversity could provide an important perspective on succession.

Relevance to Alberta's boreal forest

In the boreal forest, disturbance by fire is the primary driving force of successional initiation (Carleton and Maycock 1980, Schaefer 1993). Many species specific to this region possess reproductive mechanisms that make them adapted to frequent burns. Some reproduce vegetatively from remnant underground organs, while others use heat-induced seed dispersal and/or germination (Foster 1985). Therefore, the species composition of existing mature forest stands within

the boreal forest is primarily descended from a pioneer community adapted to a postfire environment.

The boreal forest is a rich source of wood fibre for Alberta's forest industry, and so harvesting has become an equally important source of disturbance in this region (Carleton and MacLellan 1994). Widespread industrial forestry is a relatively recent development in the history of Alberta's forests, and the primary method of timber removal to date has been clearcutting, with a small amount of seed tree or green patch retention. Changes in site conditions and vegetation communities following clearcutting have been well documented in eastern boreal forests, and in other forests in Canada (Carleton and MacLellan 1994, Harvey and Bergeron 1989, Morris and Boerner 1998, Foster 1985, Keenan and Kimmins 1993). Clearcutting can remove major portions of coarse woody material (CWM) and its associated nutrient pool (Foster 1985). Clearcutting may also disturb the litter and organic layer due to scraping, mixing and compaction. Due to the perturbation of the soil strata, which may affect percolation and reduced evapotranspiration, surface flow of water increases (Keenan and Kimmins 1993). The removal of live trees and destruction of structural elements such as snags and shading CWM on harvested sites decreases light attenuation and increases soil temperature as well (Keenan and Kimmins 1993). All of the above factors interact to provide a unique regenerative substrate in clearcut areas compared to that available immediately following natural disturbance or in an established boreal forest stand. If Grubb's regeneration niche theory holds true, the conditions found after clearcutting could precipitate a large-scale shift in species composition within the boreal forest away from that found following natural disturbance.

Natural Disturbance Paradigm

While it was not necessarily in recognition of this relationship between disturbance type and species composition in regenerating communities, forestry companies in Alberta's boreal forest have recently begun to adopt the natural disturbance paradigm. In the western boreal forest, harvesting according to this

paradigm aims to mimic the disturbance patterns caused by fire, the major source of natural disturbance in this region. By adopting this strategy, forestry companies hope to facilitate the growth of healthy postharvest communities within a landscape that closely resembles that found naturally. This appears to be even more pertinent in light of evidence that clearcut logging in Ontario's boreal forest has led to a significant change in the landscape distribution of forest community types (and therefore associated plant communities) over the last 150 years (Jackson et al. 2000).

To manage forests in a sustainable fashion, and maintain regrowth of valuable timber, the natural disturbance paradigm promotes cutting in patterns reminiscent of postfire stands; one example is leaving patches of standing timber, the natural disturbance paradigm promotes cutting in patterns reminiscent of postfire stands; one example is leaving patches of standing timber to simulate naturally occurring fire skips. However, simply copying fire patterns is not sufficient to ensure that typical postfire species will return to the area. If harvesting can be performed in way that will result in postdisturbance environmental conditions similar to those following natural disturbance that determine the regeneration niche of a site, it may be possible to produce a postdisturbance community more closely resembling that which may occur following natural disturbance.

While no suitable harvesting method has been found to date that emulates the conditions found following fire, there is another option. Namely, harvesting might be done in a way that does not return succession to the initial stages, but instead simply causes a small interruption in the ongoing process of natural succession. Partial cut harvesting may provide such an opportunity.

The potential of partial harvesting

Partial harvesting (consisting of strip cutting using narrow machine corridors) is being proposed in the Ecological Management Emulating Natural Disturbance (EMEND) study as an alternative partial harvesting method that may provide a postdisturbance environment different from that found following

clearcutting, and possibly of low enough impact that succession processes are not significantly altered. Studies of herb species distribution following partial canopy removal in deciduous forest indicate that with a loss of up to 66% of tree basal area, herb communities show no significant change in composition and distribution (Reader and Bricker 1992). Since partial canopy would be retained throughout the harvested compartments in the EMEND site, soil temperatures and moisture could potentially remain unchanged from those found preharvest. In addition, the restricted movement of harvesting equipment could reduce compaction and soil mixing, as well as propagule damage relative to clearcutting. As with other partial harvesting techniques (North et al. 1996), it would be likely that due to uneven disturbance to the propagule bank and other structural forest elements, there would be greater heterogeneity of microsite conditions than that following uniform clearcutting, possibly similar to the heterogeneous conditions found within a mature, complex-structured boreal forest stand.

This study aimed to discern whether microsite environments and understory vascular plant composition found following different intensities of harvesting (via strip cutting) differ from those found following clearcutting or in a mature forest stand, and whether or not there is a relationship between changes in environmental variables and species composition changes within treatments.

Objectives

In this study I propose to:

1. Determine changes in environment after different levels of partial harvesting.
2. Determine changes in the understory vascular plant community after different levels of partial harvesting.
3. Elucidate any relationships between changes in the environment and changes in plant community composition
4. Make some conclusions regarding the use of this type of partial harvesting by forest managers as a component of the "natural disturbance paradigm" approach to commercial harvesting.

49

Methods

Site description

The EMEND project is located in the P2 forest management area (56 deg. 44 min. N, 118 deg. 20 min. W) (Fig. 3-1). The 14 km² site consists of 10 stands divided into 100 compartments. Compartments were classified according to community type, treatment type, and replicate (see Chapter 2 for detailed description of forest types). Upland sites were chosen for sampling, and treatments were assigned to compartments semi-randomly based on ease of application. Those that were accessible for harvesting were designated as such, while compartments assigned to burn were selected based on safety factors such as natural fire breaks.

This study sampled only a portion of the EMEND site, including deciduous dominated (>75% deciduous canopy), conifer dominated (>75% conifer canopy) and mixedwood (coniferous and deciduous each 35-65%) community types, and four treatment types: control, clearcut, 20% and 75% partial harvesting. There were three replicates of each combination of treatment and forest type, with the exception of the control treatment (four replicates per forest type), for a total of 39 compartments.

Harvesting

After preharvest data collection in the summer of 1998, harvesting treatments were applied in the fall and winter of 1998, into the spring of 1999. Clearcut compartments had all canopy removed with the exception of one large and one small ellipse, 60x90m and 40x50m respectively. Ellipses of the same dimensions as those in the clearcuts were left in all harvested compartments, oriented with the longer side parallel to the machine corridors (Fig. 3-2).

75% partially harvested compartments were cleared using feller-bunchers to cut 5m machine corridors interspersed with 15m leave strips. Machine corridors were oriented north-south to minimize blowdown. Skidders then dragged felled trees down the machine corridors to landings. 20% partially harvested compartments were also cleared with feller-bunchers and skidders.

However, after clearing all of the trees from the 5m machine corridors, loggers then randomly thinned the leave strips (discriminating neither by stem size or location within the strip), leaving an overall compartment stem count approximately 20% of the original.

Plot location

The same 312 permanent plots were used in 1998-2000 (Fig. 3-3), with layout as described in chapter 2, with the exception of those that could not be found due to damage caused by the harvesting process. In cases where rebar could not be found in 1999, plots were reset using the same baseline location as before. In some cases, plots interfered with other EMEND research projects and were relocated in 1999 (see Appendix 1 for plot relocations).

Understory and canopy vegetation sampling

Sampling of all vegetation was done using the same procedures in 1998-2000, as outlined in Chapter 2.

Environmental Variables

Environmental measures were taken in 1999 and 2000 using the same methods as outlined in Chapter 2, with the following exceptions.

In 1999 and 2000, resin bags contained 35 mL of IONAC NM-60 mixed bed exchange resin. Resin bags were agitated in 2N NaOH for one hour (1L/20 bags), rinsed in deionized water, then agitated in 2N NaCl for one hour. Bags were then repeatedly rinsed in deionized water until rinse water had a neutral pH, and were kept refrigerated until buried. Bags were extracted in 2N NaCl. In all years, resin was removed from the bag, mixed with 100 mL of the extract solution, agitated on a bed shaker for 90 minutes, and then filtered.

Litter type within the herb plot was also assessed in 1999 and 2000 as being predominantly one type of a 7-stage type classification (See Appendix 2). A proximity class was also assigned to each plot post-harvest indicating its overlap with the nearest machine corridor (See Appendix 2).

Analyses

All conversions and proofing of data were done in Excel (Microsoft 2000). Summary statistics were calculated for the species data including shrub, herb and total understory species richness and diversity (per plot and per compartment). Diversity was calculated using the Shannon-Weiner index:

$$H'=\Sigma p_i * \ln p_i,$$

and the Simpson's index:

$$D= \Sigma(p_i^2),$$

where p_i is the proportional abundance of species i within the unit area, the prior index being more influenced by rare species, the latter by dominant species (Boyle 1991).

All of the canopy structure and environmental variable data, as well as richness and diversity indices (per plot and per compartment) were analyzed using SAS software. Each environmental, canopy and species index variable was analyzed separately using a repeated measure general linear model (PROC GLM) analysis of stands nested within a 3X4 factorial experimental design (α=0.05) to investigate variation related to time (see Table 3-1 for fixed and random factors). Variation among treatments within years was determined within the general linear model using least squared means comparison tests (*lsmeans/pdiff* function in SAS).

Frequency distributions were constructed for CWM decay classes to determine whether there was variance in the proportion of each decay class with application of the treatments. Litter type was not analyzed using repeated measures, since it was only measured postharvest. All of the year 2000 canopy structure and environmental variables, including litter type, were analyzed to determine their relative importance in discriminating each treatment.

52

Discriminant function analysis (DFA) was used to determine, with a stepwise forward selection of variables, which variables explained the majority of variance among treatments. This analysis was performed using SPSS version 10.0 software (SPSS Inc. 1999).

Species data were preliminarily analyzed by correspondence analysis (CA), using CANOCO for Windows version 4.0 software (ter Braak 1987a), to determine whether forest types were segregated, and whether their relative species composition changed over time. After viewing initial CA ordinations, detrended CA (DCA) was used instead of CA, to reduce 'arch effect'. This pattern is a product of a quadratic relationship between the axes that compresses and therefore disguises relationships within the ordination; detrending eliminates this confounding effect (ter Braak 1987b). Ordinations for each year were checked for grouping with relation to community type. Then, separate DCAs were done for each community type within each year.

Detrended canonical correspondence analysis (DCCA) was also used to analyze species distribution, but this method uses environmental variables to constrain the axes along which plot scores are graphed. Ordinations of plot scores were created to determine whether plots segregated by treatment over time. Ordinations of environmental variables were also plotted, to determine the relative contribution of each variable to the construction of each axis.

PROTEST analysis (Jackson 1995) is a randomized fit test which can be used to compare two matrices using generalized rotational fit; it is useful in comparing communities over time in a quantitative fashion, which DCCA alone cannot do. The analysis was performed using 9999 randomized permutations on the DCCA plot scores of each treatment within each year and forest type to determine objectively whether the matrices were significantly different over time. PROTEST offers an advantage over the more commonly used Mantel test by eliminating intermediate steps of calculating distance matrices (Jackson 1995).

Data from compartment 926 (conifer dominated control) was excluded from analysis, since the compartment was burned in the summer of 1999. Because of this missing data, degrees of freedom for analyses involving the

53

conifer-dominated community were slightly different from those in the other community types.

Results

Change in forest structure with varying levels of harvesting

Patterns in live density and basal area indicate that the treatments were applied as intended (Fig. 3-4). In the first year postharvest, basal area measurements show significantly different values between all treatments. Basal area was lowest in the clearcut, highest in the control, with the partial harvests showing intermediate values; all treatments were significantly different. This same pattern was found in the second year postharvest. Live density showed similar patterns, except 75% and controls were not significantly different in the first year postharvest. By the second year, all treatments were significantly different. Canopy cover values showed an overall decrease postharvest, even in the controls, likely due to a different team taking the measurements preharvest. The relative values of canopy cover across treatments within years showed the same pattern as live density and basal area, with lowest values in the clearcuts and highest in the controls in the first year postharvest.

The 20% partial harvest, by the second year postharvest, had values for live density and basal area that were very similar to those in the clearcuts. That was likely due to the high rates of blowdown in the 20% compartments. A decrease in density in the 75% harvest between first and second year postharvest suggested that there was some blowdown in that treatment as well.

None of the forest types showed significant variance over time in snag density among treatments in repeated measures analysis (Table 3-2). However, there were significant differences between treatments in the postharvest years in the conifer community. Graphs of the mean snag density for each forest type indicated that patterns were similar for each forest type, with magnitude being the major difference between types. Therefore, a single graph was made for all forest types, showing that snag density had a similar pattern to that of live density, with control treatment density significantly higher than all other

54

treatments postharvest, and clearcut density was significantly lower than 75%
and control treatment densities (Fig. 3-4). While this is an expected result, it
cannot be considered conclusive due to the fact that there were significant
differences among treatments preharvest.

Change in environmental variables with various levels of harvesting

The only abiotic environmental variables that showed consistent patterns
of variation among treatments across all forest types were soil temperature and
moisture (Figure 3-5). Temperatures at the 10 cm depth were significantly
different in all treatments, highest in clearcuts and lowest in controls, while 30
cm depth temperatures showed grouping similar to that found in live density
and basal area. The 20% partial harvest and clearcuts had similar values to each
other; those treatments had higher values than the 75% and controls, which were
also similar to each other. Moisture showed this clustering in the first year
postharvest, but by the second year the only significant difference was between
clearcuts and controls. There were significant differences among treatments
preharvest, but these were very small in magnitude. Though there were
significant differences in available PO_4^{3+} and NH_4^+ among treatments in some
forest types in some years (Table 3-2), graphs showed no patterns relating to
treatment.

Distribution of CWM decay classes was also uniform across all forest
types (Fig. 3-6). The proportion of CWM in more advanced decay classes (4-7)
was greater than 50% in all treatments preharvest. In the first year postharvest,
the proportion of CWM in lower decay classes (1-3) was much greater in the
clearcuts and 20% partial harvest (proportion is >90%), greater in the 75% partial
harvest (~80%), and the controls as well (~75%). In the second year postharvest,
the proportion of CWM in lower decay classes had decreased appreciably in the
clearcut (proportion is <55%) and control (<40%), and moderately in the 20%
partial harvest (<75%) and 75% partial harvest (<65%). These large changes in
proportions can not reasonably be explained by decay alone, so some of the

changes may be attributed to errors in data collection, possibly due to the subjective nature of the decay classification.

Other environmental variables showed significant changes over time, but varied differently in each forest type (Table 3-2). ANOVA results indicated that the average number of CWM pieces per plot, and the total CWM percent cover per plot varied significantly among treatments over time in the deciduous dominated community, while only number of pieces varied significantly in the mixedwood community. Least squared means comparison of treatments within years indicated that in the first year postharvest, clearcuts and 20% harvests had a higher number of pieces than the other treatments in all forest types (Fig. 3-7). However, only clearcuts in the deciduous and mixedwood communities had numbers significantly higher than in the control.

While CWM percent cover had significantly different values among treatments within the first year postharvest in the conifer dominated and mixedwood communities, and in the second year postharvest in the deciduous community, there was no apparent pattern to the values (Fig. 3-7). When variance over time was viewed, there was little change in the CWM cover with the exception of a drop in cover pre- to postharvest in the mixedwood 75% harvest, and an increase pre- to postharvest in the deciduous 75% harvest. A decrease in CWM cover may not be expected, but it can be explained by the removal of CWM by loggers, or fragmentation of CWM into smaller pieces by machines.

Discriminant function analysis of the environmental variables was completed to determine which variables could be used to predict to which treatment a given plot would be categorized. The overall differences in environment among treatments were not strong or predictive. The most important variable discriminating treatments in all forest types was litter type, followed by CWM variables and available PO_4^{3+}, with little to no contribution by soil temperature and moisture variables (Table 3-3). The exception was the coniferous community, where soil temperature at 10cm had the third highest correlation value; this community's discriminant function also had the lowest

56

eigenvalue (0.369), indicating that the environmental variables were relatively weak discriminators of the treatments in this community. The eigenvalues were higher for the mixedwood (0.643) and deciduous community (0.542). In all communities, cross-validation to determine the ability of the variables to classify each treatment showed a poor success rate, with all communities having success percentages equal to or less than 50% (deciduous=50.0%, mixedwood=48.5%, coniferous=40.4%). This can be compared with the chance of classifying them correctly purely by chance which is 25%.

Change in understory plant community with various levels of harvesting

Responses of the understory community to harvesting were forest type specific. Changes in plant community composition following harvesting were less in partial harvesting treatments than in clearcuts.

Detrended correspondence analysis of species abundance

DCAs using per plot species abundances produced ordination diagrams too cluttered to analyze clearly (312 plotted points), therefore per compartment species abundances were used instead to construct the matrices, with one sample representing each compartment (Fig. 3-8). In all three years, deciduous-dominated compartments stayed segregated from mixedwood and coniferous dominated communities, which overlapped considerably in all years. Within each cluster, compartments shifted somewhat over time but maintained segregation.

Cover, richness and diversity indices per plot

Percent cover of the herb and shrub layers and of the total understory were calculated to determine whether the harvesting types caused significant loss of understory biomass. There were no significant time *treatment interactions of percent cover in any layers in any forest types, with the exception of the total understory layer in the deciduous community (Table 3-4).

Understory cover was substantially reduced in harvested treatments, with the greatest reductions occurring in clearcut and 20% partial harvest

57

treatments. However, mean per plot cover values were also significantly different among treatments preharvest in some layers in the deciduous and coniferous forest types (Fig. 3-9). For this reason, postharvest patterns, while they appear to correspond with harvesting treatments, cannot be considered solely a product of harvesting. In the deciduous community, both the shrub and total understory layers of the control treatment had significantly greater mean cover than the 20% partial harvest, with the shrub control also significantly greater than the clearcut. Understory cover in both the mixedwood and coniferous communities showed similar patterns, with clearcuts having the lowest mean cover and controls having the highest. The mixedwood herb and total understory layers were an exception, where the 20% partial harvest had the lowest mean cover. In all cases, the 75% partial harvest mean cover values were intermediate between the control and the treatment with the lowest cover values.

Richness per plot showed a significant time*treatment interaction in the shrub layer of the deciduous dominated communities, and in the herb and total understory in the coniferous community (Table 3-4).

In the conifer and deciduous dominated communities, there were no significant differences in mean per plot richness among treatments in the preharvest year (Fig. 3-10). In the deciduous dominated community, mean herb richness in the control was higher than in the clearcut and 75% harvest by the second year postharvest. Significant differences between the clearcut and 75% treatments in the deciduous shrub layer disappeared by the second year postharvest. The combined effect of these contrasting responses was that total species richness did not differ substantially between treatments. In the coniferous community, there were some significant differences among treatments in the herb and total understory layers. Only the mean richness in the clearcut treatments was significantly different, lower than that in all other treatments.

The mixedwood community showed significant variance among treatments in the total understory layer preharvest (Fig. 3-10). By the second year postharvest, there was no significant difference among treatments in the shrub layer, while the mean herb and total understory richness was highest in the

controls and lowest in the clearcuts. All treatments were significantly different, with the exception of the 75% partial harvest that was intermediate between control and 20% harvest treatments. The mixedwood controls showed little change over time in per plot richness values, while the clearcut and 20% harvests generally exhibit a drop in value from pre- to post harvest.

While Shannon-Weiner diversity stayed fairly stable over time in the deciduous community, the mixedwood and conifer communities experienced drops in understory diversity, particularly in the clearcut treatments (Fig. 3-11). There were significant time*treatment interactions in the shrub layer Shannon-Weiner (SW) diversity in the deciduous forest type, and in the herb layer in the coniferous community (Table 3-4). Mean SW diversity per plot was not significantly different among treatments in any forest type or layer (Fig. 3-11). In the first year postharvest, mean SW diversity per plot for the herb layer and total understory in the clearcuts had dropped substantially from preharvest diversity in both the mixedwood and conifer dominated sites. Shrub layers in both of these communities showed no apparent pattern of variance over time. The deciduous community exhibited somewhat different patterns, where mean SW shrub diversity per plot was slightly higher in clearcut and 20% partial harvest than in the 75% harvest and control treatments by the second year postharvest.

Simpson's diversity index (SI) was significantly different among some treatments, but the patterns were masked by the large standard errors of some treatments, indicating substantial variance among plots within treatments. Per plot SI showed no significant time*treatment variation in any forest type (Table 3-4). Mean SI per plot varied substantially within treatments (large standard errors). The mixedwood community had significant differences preharvest among treatments in the shrub layer (Fig. 3-12). The clearcuts generally exhibited higher SI values than the other treatments in the mixedwood and conifer communities (Fig. 3-12).

Richness and diversity indices per compartment

At the compartment level, richness and diversity indices showed a lesser magnitude of variation over time among treatments. Mean herb richness per compartment in the deciduous community showed no significant differences among treatments in any year (Fig. 3-13). Herb richness showed a significant time*treatment interaction as well as a time*forest type interaction (Table 3-5). In the mixedwood and conifer dominated communities, clearcuts showed significantly lower herb richness than in any other treatment in both the first and second postharvest years (Fig. 3-13). There were some significant differences among treatments for the shrub layer of mixedwood forests in the first preharvest year, but there were no other significant differences among treatments in the shrub layer of any community. Total understory species richness per compartment showed a time*treatment interaction (Table 3-5), but the only significant difference shown by the least squared means analysis was in mean richness values among mixedwood treatments in the first year postharvest in which clearcuts had lower richness than controls (Fig. 3-13).

The only significant differences among treatments over time in the SW diversity per compartment were for the total understory diversity (Table 3-5). Least squared means comparison of SW diversity per compartment in the mixedwood community showed clearcuts were significantly less diverse than controls in all layers, but only in the first year postharvest (Fig. 3-14). In the conifer dominated community, clearcuts were less diverse than all other treatments, but only in the total understory in the first year postharvest. Treatments within the deciduous community showed no significant differences. Simpson's diversity per compartment showed no significant differences among treatments over time (Table 3-5).

Relationship between plant community patterns and environmental patterns

Detrended canonical correspondence analysis (DCCA)

Detrended canonical correspondence analysis of per plot species abundances showed that treatments segregated over time; moreover, the mixedwood and conifer communities showed a greater contribution of environmental factors to the segregation between treatments. DCCAs of the preharvest species abundance scores showed no separation of treatments (Fig. 3-15). By the second year postharvest, treatments were partially segregated, with clearcut plots clustering at the lower end of the primary axis (Fig. 3-15), negatively correlated with basal area in the mixedwood and conifer communities and with canopy cover in the deciduous community (Fig. 3-16). The clearcuts were positively correlated, but to a lesser extent, with CWM variables and soil temperature at 30 cm in all forest types. Partial harvests were clustered, but showed more overlap with the controls than the clearcuts. Clusters of 20% harvest plots tended to be slightly lower on the primary axis than the 75% partial harvest or control treatments.

The species composition of the stands within each community, however, showed a contrasting pattern to that of the treatments, starting with relatively separate clusters of plots for each forest type, and becoming desegregated by the second year postharvest (Fig. 3-17). Preharvest plot scores showed separation of stands along the primary axis within each forest type, indicating site-specific understory composition within forest types. Postharvest, and especially by the second year postharvest, stands in the deciduous community showed complete overlap of clusters, while the mixedwood and coniferous communities showed increased, but not complete, overlap of plot scores among stands.

PROTEST analysis

PROTEST analysis of DCCA plot scores indicated higher levels of similarity between years in the two treatments with greatest retention of canopy (Table 3-6). PROTEST analysis is unusual because a lower p-value indicates a greater similarity among matrices. Controls in all forest types showed a high level of similarity across all years ($p \leq 0.0002$), while clearcuts showed the greatest

dissimilarity across all years (1998-2000) in deciduous dominated (p=0.1300) and conifer dominated (p=0.1661) communities, with 20% partial harvests showing a substantial loss of similarity in the deciduous community (p=0.1243). However, 20% partial harvest treatments in the coniferous community stayed quite similar after harvesting (p=0.0191). In the mixedwood community, both clearcuts and 20% partial harvests showed high dissimilarity over time (p=0.0741 and p=0.0756 respectively). With the exception of the conifer community, where 75% partial harvest matrices were less similar than the 20% (p=0.0329), 75% partial harvests had values falling in between controls and the other treatments (deciduous p=0.0609 and mixedwood p=0.0553).

Discussion

Overall, results indicated that, while there were some environmental variables and plant community properties that changed with application of harvesting treatments, there were no strong relationships between the changes in the environment and the changes in the plant community. There was evidence that some changes in the environment and plant community were forest-type specific. In addition, partial harvesting techniques showed potential as an alternative to clearcutting, especially in deciduous communities, since changes in plant community composition after partial harvesting were less substantial than in clearcut treatments.

Effects of partial harvesting on forest structure and environment

Effects on forest structure

Immediately following harvesting, measures of canopy cover, basal area and live density verified that the partial harvesting treatments were applied as intended; however, blowdown proved to be a major concern in the feasibility of the strip harvesting process. The exposure of trees that have not been wind-hardened to substantial wind force is an acknowledged weak point of partial harvesting techniques (Coates 1997). At EMEND, weather patterns varied considerably across the three seasons of this study, varying from dry and hot in

1998, to cool and very wet with approximately 10 days total with no precipitation in the months of June through August in 2000 (pers. obs.). This substantial increase in precipitation may also have contributed to the severity of blowdown on the research site (Wilson and Bowman 1987). Regardless of the cause, the loss of residual canopy, especially in the 20% treatment, may mean that the complex and more labour intensive harvesting pattern might not be considered worthwhile unless the short-term retention of canopy, or the CWM resulting from the blowdown, has a significant effect on the long-term community structure. Alternately, the stem selection process during harvesting could be non-random, with harvesting crews selecting more windfirm trees based on height-diameter measures, and crown form (Navratil 1995).

Effects on other environmental variables

Soil moisture and temperature

As expected, the level of canopy removal significantly influenced the forest environment. As has been found in previous studies, soil temperature and surface moisture levels increased in clearcuts in relation to uncut areas (Keenan & Kimmins 1993, Bird and Chatarpaul 1988, Cortina and Vallejo 1994); furthermore, the intermediate values for these variables in the partial harvests suggests that these variables are strongly correlated with the percent of canopy removed. This is not surprising, since both of these variables are strongly influenced by canopy cover (Kimmins 1987). The increased penetration of radiation to the ground level was the likely cause of increased soil temperature, while the loss of canopy trees lowered the per area transpiration rate and canopy interception, increasing the amount of available water (Black et al. 1980, Bréda et al. 1995)

Nutrients and CWM

CWM cover and piece count were correlated with treatments as well, but not as consistently across forest types. The initial increase in number of pieces of

CWM in the clearcut and 20% harvests was expected, since the machine operators may have unintentionally left some standing dead or fallen stems on site, left branches due to breakage and possibly left low quality stems intentionally. In addition, blowdown may have contributed to postharvest CWM, if trees exposed by harvesting were not windfirm (Coates 1997). There was less of an increase in CWM in the 75% site; this may have been due to the fact that removal was simpler, with operators not having to reach for or swing trees into the corridor for extraction. By the second year postharvest, number of pieces dropped in the clearcuts and 20% harvest, partly due to increases in decay rate associated with greater temperature and moisture as mentioned above. This is supported by the rapid progression of lower decay class CWM in the first year postharvest into higher decay classes in the second year postharvest in clearcuts, less so in the 20% harvests. However, the magnitude of change in CWM decay classes seems high to be solely attributed to this, and may be a result of errors in data collection

Based on existing studies on nutrient response to clearcutting (Roberts et al. 1998, Bird and Chatarpaul 1988, Cortina and Vallejo 1994), one might have predicted a change in available nutrients following the various harvesting treatments, possibly due to increased decomposition caused by increased soil temperature and moisture (Freedman et al. 1996), although there have been contradictory findings (Bird and Chatarpaul 1988). The lack of apparent pattern in nutrient concentrations can be accounted for. While nitrogen-containing ions are acknowledged as a possible limiting nutrient in the boreal forest, these forests are also known to be highly adaptable to changing nitrogen levels (Barbour et al 1987, Kimmins 1987); in addition, available pools of each of these nutrients are affected by multiple factors. Available nitrogen (NO_3^- and NH_4^+) can be affected by changes in plant uptake, soil microbial activity (Vesterdal et al. 1995) and mineralization rates (Morris and Boerner 1998), as well as type, quality and quantity of litter (Roberts et al. 1998); moreover, the availability of NH_4^+ as measured by the resin can fluctuate with variation in precipitation and soil

moisture (Binkley 1984). Therefore, it was expected that the concentrations of these ions would vary considerably among microsites.

Overall difference in environment among treatments

While patterns were evident in environment response to harvesting, the overall differences in environment among treatments were neither strong nor predictive. Based on the patterns of response in environmental variables to the harvesting treatments, any plant community response that correlated with the four different levels of canopy removal might be related directly to canopy removal or to closely corresponding soil temperature or soil moisture. Based on the results of the discriminant function analysis, however, environmental variables cannot be consistently used to classify the treatments; therefore, it is less likely that plant community changes related to treatments were effected by changes in the environment like moisture or temperature.

Effect of partial harvesting on the understory plant community

The results indicated that, while some environmental variables such as soil temperature and moisture experienced a strongly correlation to canopy removal across all forest types, understory community structure responded to the harvesting treatments in a community-specific fashion. According to some studies, the high diversity of the deciduous community should have made it more resilient to disturbance than the other forest types (Connell 1978, Franklin et al. 1989); however, this point has been disputed (eg. MacMahon 1980) and my results did not support this expectation. Regardless, the deciduous community richness and diversity were significantly different from the mixedwood and conifer forest types, suggesting the potential for this community to respond differently to disturbance. Response of the deciduous community to harvesting verified this prediction.

65

Cover

With the substantial machine disturbance caused by harvesting, it would be expected that many of the understory plants would be damaged or destroyed. Although some studies have found that understory plants are very resilient and often grow back from surviving roots, rhizomes or seeds within the first couple of years after harvesting (Qi and Scarratt 1998, DeGrandpré et al. 1993), the expectation was for at least a temporary decrease in understory cover. Indeed the data showed this, but there was a difference in the recovery of each community. By the second year postharvest, the herbaceous understory cover of the deciduous community clearcuts and 20% harvests was already showing recovery towards the 75% and control treatments, while the cover values of the clearcuts and 20% harvests stayed lower in the mixedwood and conifer communities. Herbs that are found beneath deciduous canopies are likely able to grow in areas with substantial shifts in light availability, since they already experience large changes in light regime spatially and seasonally (Constabel and Lieffers 1996, Lieffers et al. 1999); therefore, the changes in light regime after harvesting might not have affected their growth.

In addition, the shrub community actually showed an increase following harvesting. This is an excellent example of the interplay of multiple layers in light dynamics (Riegel et al. 1992). Shrubs are typically more plentiful under deciduous canopies than coniferous ones, and shrubs then contribute to light attenuation at herb layer and ground levels (Constabel and Lieffers 1996, Messier et al. 1998). The tradeoff between these layers following harvesting may have maintained a fairly constant amount of light at ground level, keeping a stable light environment for the herb layer. This is especially likely since reduced machinery damage in the partial harvest compared to the clearcuts could have minimized shrub mortality.

Richness and diversity

In mixedwood and coniferous forest types, partially harvested stands maintained higher diversity than the clearcuts; furthermore, the deciduous community's diversity remained fairly stable over time regardless of treatment. Richness showed similar patterns, with the exception of the partial harvests in the mixedwood community, which showed a slight drop in richness in the herb layer and overall understory. Existing studies have indicated that some deciduous communities have little to no environmental or understory compositional response to canopy removal (Roberts and Gilliam 1995a, Reader and Bricker 1992, Yorks and Dabydeen 1999). One explanation of the lack of response to canopy removal in these forests was the open habit of the canopy in a mature stand that allowed high light penetration prior to removal (Roberts and Gilliam 1995a).

In addition, the seasonal differences between deciduous and coniferous canopies as described above could contribute to differences in community response to treatment. The similarity of response between the mixedwood and conifer communities (and the general overlap of species composition of these two forest types in the DCA) may be due to similarity of light regime beneath these two canopy types. Previous data has indicated that light beneath a mixedwood canopy does not always have an intermediate level between deciduous and conifer below-canopy light levels. Due to the angle of incidence of sunlight in northern forests, the conifer component of mixedwood canopies intercepts a larger fraction of that light, creating a light environment more similar to that beneath a conifer canopy (Constabel and Lieffers 1996).

The smaller magnitude of variance in richness and SW alpha diversity among treatments at the compartment level suggests that the sum of changes at the plot level, while they may seem dramatic at a small scale, actually have a much smaller effect on the overall species diversity of the compartment than first impressions suggest. This suggests that changes in environment that change the regeneration niche may occur at the microsite scale instead of the compartment or stand scale, and that this fine scale variation 'averages out' over larger spatial scales.

It is worth noting that while there was a significant drop in richness and diversity in the first year postharvest in the conifer and mixedwood partial harvests, the trend was toward recovery of those values to preharvest levels. Some existing studies of understory response following harvesting have also found that there was no significant change in understory diversity following harvesting (Fredericksen et al. 1999). However, while the differences among partial harvest and control treatments were no longer significant by the second year postharvest, the mean herb layer and overall richness and diversity values within the clearcuts continued to be somewhat lower. This suggests that, while understory communities in clearcut forests lacked resilience, partial harvests as applied in this study may have fulfilled the goal proposed by Lieffers et al. (1999) to strike a balance between increased resources and increased competition. Partial harvesting could provide the resources necessary to allow new growth without creating environmental extremes or encroachment of competitors.

Changes in community composition

Some studies to date of partial harvesting indicate that species richness or diversity in understory communities do not change substantially post-treatment (Fredericksen et al. 1999, Beese & Bryant 1999), while others found that shifts in diversity in understory communities due to partial harvesting persisted for decades afterward (Alaback & Herman 1988). In this study, the smaller decrease of diversity in partial harvest communities versus that in clearcuts in response to treatment should not be adopted as evidence those communities are not changing pre- to postharvest. Though diversity values were fairly stable following partial harvest treatments, and even in the deciduous dominated clearcuts, this does not address invasion or disappearance of specific species or all changes in dominance and composition (Boyle 1991). The segregation of treatment DCCA scores indicated that, while diversity was not changing substantially, the species composition was changing in the deciduous clearcuts. Understory communities, instead of experiencing an influx or loss of species, were simply experiencing shifts in abundance of species that were already

68

present (Halpern & Spies 1995). In addition, results of PROTEST analysis show that matrices of 20% partial harvests in both the deciduous and mixedwood communities were changing as much pre- to postharvest as the clearcuts. It is important to note, however, that this analysis does not show the magnitude or direction of shifts in these matrices.

Drivers of change in community composition

DCCA analysis does show the importance of environmental variables in the changes in community composition. Overall, low eigenvalues of the DCCAs suggested a fairly weak relationship between environmental variables and plant community composition, which has been found in other studies following natural disturbance (Degrandpré et al. 1993) and harvesting (Rubio et al. 1999). However, results indicated that the changes in the conifer dominated and mixedwood communities were more strongly related to changes in the environment than were changes in the deciduous forest.

Low eigenvalues of some of the DCCA ordinations, especially those in the deciduous forest, as well as discriminant function eigenvalues, indicate that other environmental factors that were not measured might yield a better account of variance within the species distribution. It is possible that persistence of species within a given community may be more dependent on reproductive potential, such as seed banks (Lewin 1986, DeGrandpré et al 1993) *sensu* initial floristics theory (Egler 1954) or long-term prevailing edaphic conditions (Harvey et al. 1995), than the environment created by a given disturbance. In one study, results indicated that while understory composition was related to existing soil conditions and application of silviculture treatments, there was no apparent connection between silviculture treatments and soil conditions (Rubio et al. 1999). This suggests that while soil conditions and canopy may both affect understory composition, it may not be in a linear relationship of canopy affecting environment which in turn influences understory.

Some studies suggest that previous presence/absence of a species is the strongest predictor of post-disturbance herbaceous community structure

(Halpern 1988, Hughes and Fahey 1991). Another study suggests that the coincidence of over and understory communities is primarily due to common site requirements (Carleton & Maycock 1980) not due to any effect of canopy on understory or vice versa. This may be an indication that reproductive potential in the form of propagule banks is as important a determining factor as canopy removal or associated environmental changes in determining the post-disturbance community composition (Hughes and Fahey 1991). For this reason, partial harvest, may be a useful alternative to clearcutting, since soil disturbance is limited to ¼ of the land area harvested; this is reflected in the lesser effect of partial harvesting on diversity and richness values than that seen in clearcuts. It is also reflected in the similarity of changes in diversity from pre- to postharvest between 20 and 75% harvest, which may be because the amount of ground disturbance in both partial harvest treatments is the same.

In the conifer community, eigenvalues of the DCCA ordination were substantially higher than for other forest types; this may indicate a greater importance of canopy in determining understory composition in this forest type. This does not disagree with the above studies that propose previous community composition is the most important determining factor in future community composition.

According to Grubb's regeneration niche theory (1977), a plant may only establish if a propagule is present, and if the niche is available in which to succeed. In these cases, specific pools of propagules were available in each forest type, and even in each stand; this factor may be independent of canopy composition (see Chapter 2). For these propagules to establish, the correct niche must be available for it to succeed. In the case of the deciduous community, the lack of significant change in understory diversity in any of the harvest treatments may have been due to the prevailing conditions under a closed canopy ie. the qualities of the niche important to the establishment of those propagules was not changed enough by harvesting to alter community diversity. For example, deciduous understory communities typically experience a higher ambient light level than communities underneath conifers (Constabel and Lieffers 1996,

70

Lieffers et al. 1999); moreover, seasonal fluctuations in leaf cover due to autumn leaf drop provide a wide range of light conditions over time (Ross et al. 1986). Thus, the increased light penetration caused by partial harvesting may not have been enough to create a new niche.

In the mixedwood and coniferous communities, the denser quality of spruce canopy may mean that the niche was changed more substantially by its removal. Light conditions vary beneath different types of canopy; light attenuation is greater beneath a coniferous canopy than under a broadleaf canopy (Constabel and Lieffers 1996, Lieffers and Stadt 1994, Lieffers et al. 1999). Therefore, removal of canopy containing conifers is likely to precipitate a greater change in light conditions at ground level than removal of a deciduous one. This may explain why the DCCA in these communities explained a greater proportion of the variance among treatments.

Scale of influence is also important to address. While per plot or per compartment diversity index values may suggest that diversity is being preserved, landscape heterogeneity may be affected. Stands that had highly segregated DCCA scores preharvest, had scores that overlapped considerably postharvest. In other words, while species composition may be preserved on a small scale, the landscape mosaic may be altered considerably. Changes may occur in terms of loss of a particular type of forest (Spies et al. 1994), an increase or decrease in the size of forest patches, or a general change in the heterogeneity of forest types and sizes (Mladenoff et al. 1993). Landscape-level distribution of community types is an important component of biodiversity that some researchers say is as necessary to consider as species diversity (Boyle 1991, Galindo-Leal and Bunnell 1995, Kimmins 1997), in part because of the effects of landscape patterns on resident wildlife (Hansen et al 1991, Haila 1994), especially those dependent on understory habitats, such as birds (Willson and Comet 1996) and phytophagous insects (Murdoch et al. 1992). All of these factors are components of ecosystem process, another aspect of forests that needs to be considered in preservation of biodiversity (Franklin 1998).

Implications for biodiversity management

The plant community associated with the deciduous canopy stayed segregated from the other communities in DCA both before and after harvesting. Based on this alone, one might suppose that homogenization of forest types is not an issue in regards to harvesting. However, based on the response of plant communities among stands within forest types, homogenization is a concern. The understory plant community composition within stands is altered with application of harvesting such that the landscape mosaic of forest types may be altered considerably.

While preharvest stands exhibited a more heterogeneous pattern of overall plant communities, where each stand within a forest type possessed a unique community of shrubs and herbs, a more homogeneous distribution began to appear postharvest, with stand understory communities overlapping considerably within each forest type. This suggests possible creation of within compartment fragments, consisting of machine corridors and leave strips, which would result in a mosaic of much smaller pieces. Since plots were not classified at this scale, no patterns were evident in the analysis. Alternatively, the mosaic may be rearranged so that areas of treatment become new 'stands', while the original stand structure disappears, causing a redistribution of the mosaic at a slightly larger scale.

Recent studies propose that aspen-dominated communities may not be an early successional stage preceding a mixedwood or coniferous forest as previously suggested, but are instead a unique successional pathway (Cumming et al. 2000, Bergeron and Dubuc 1989). This supports recent suggestions that harvesting methods that intend to mimic natural disturbance should consider not just patterns of natural disturbance, but should instead incorporate the unique successional patterns and processes of each community on a site-specific basis (Roberts and Gilliam 1995b, Galindo-Leal and Bunnell 1995) with attention given to determining patterns of natural variation (Haila 1994). While this study does not confirm the long-term successional patterns of the site, results suggest that the establishment and success of understory species after partial and total

canopy harvesting may be different in different forest types, emphasizing a need to approach harvesting in each community with respect for its unique properties and processes.

Table 3-1. Experimental design used in general linear model analysis for analysis of a) the total data set and b) each forest type separately.

a)

Variables	Error	Designation
Forest Type	Stand (Forest Type)	Fixed
Stand (Forest Type)	Plot (Stand (Forest Type) *Treatment)	Random
Treatment	Stand (Forest Type)	Fixed
Plot (Stand (Forest Type) *Treatment)		Random subsamples
Time	Time*Stand(Forest Type)*Treatment	Fixed
Forest Type*Treatment	Stand(Forest Type)*Treatment	
Stand(Forest Type)*Treatment	Plot (Stand (Forest Type) *Treatment)	
Time*Forest Type	Time*Stand(Forest Type)	
Time*Stand(Forest Type)	Plot (Stand (Forest Type) *Treatment)	
Time*Treatment	Time*Stand(Forest Type)*Treatment	
Time*Stand(Forest Type)*Treatment		

b)

Variables	Error	Designation
Treatment	Compartment (Treatment)	Fixed
Time	Compartment (Treatment)	Fixed
Compartment (Treatment)		Random samples
Time*Treatment	Time*Compartment (Treatment)	
Time*Compartment (Treatment)		

Table 3-2. Repeated measures analysis of variance comparing pre and post harvest canopy structure and environmental variables within each forest type. Significant adjusted Pr > F values (p≤0.10) indicate significant variance over time (time), over time among treatments (time*treatment) and among treatments within each year (treat). Italicized values are considered significant. To avoid pseudoreplication, the 8 per plot values per compartment were averaged prior to analysis.

	Deciduous dominated					Mixedwood					Conifer dominated				
	Time	Time* Treat	Treat			Time	Time* Treat	Treat			Time	Time* Treat	Treat		
			Pre	Post 1	Post2			Pre	Post 1	Post2			Pre	Post 1	Post2
Numerator d.f.	2	6	3	3	3	2	6	3	3	3	2	6	3	3	3
Error d.f.	16		8			16		8			14		7		
Canopy structure															
Live density	*0.0095*	0.7516	0.9616	*0.0494*	*0.0620*	*0.0213*	0.3043	0.8486	0.1515	0.1155	*0.0026*	0.3671	0.9179	0.3798	0.3018
Basal area	*0.0001*	*0.0003*	0.7136	*0.0289*	*0.0361*	*0.0001*	*0.0001*	0.3937	*0.0001*	*0.0001*	*0.0001*	*0.0001*	0.6619	*0.0062*	*0.0090*
Canopy cover	*0.0001*	*0.0060*	0.6383	*0.0001*	*0.0679*	*0.0001*	*0.0001*	0.6784	*0.0002*	*0.0001*	*0.0001*	*0.0019*	0.7629	*0.0045*	*0.0119*
Snag density	*0.0023*	*0.0805*	0.1361	0.6469	0.6469	0.1026	0.1121	0.1725	0.2344	0.2624	*0.0183*	0.5041	0.8641	*0.0951*	0.0686
Environmental variables															
Soil temp. – 10cm	*0.0007*	0.7098	0.9344	0.4908	0.2915	*0.0005*	*0.0919*	0.9271	*0.0090*	*0.0188*	*0.0001*	*0.0400*	0.5700	*0.0419*	*0.0313*
Soil temp. – 30cm	*0.0001*	0.7119	0.9082	*0.0500*	0.1457	*0.0001*	*0.0914*	0.9998	*0.0294*	*0.0068*	*0.0001*	*0.0340*	0.2369	0.1051	0.1418
Soil moisture	*0.0001*	0.3033	0.5449	*0.0852*	0.6673	*0.0001*	0.7298	0.4276	0.2064	0.6325	*0.0001*	0.2981	0.3218	0.7772	0.7846
CWM (per plot)															
Avg. diameter	*0.0897*	0.3747	*0.0441*	0.1303	*0.0890*	0.7756	0.2801	0.7253	0.9751	0.9197	0.2409	0.2821	0.7655	0.1587	0.7008
# of pieces	*0.0001*	*0.0930*	*0.0141*	*0.0203*	*0.0294*	*0.0102*	*0.0129*	0.5271	0.2224	0.6998	*0.0416*	0.8305	0.8477	0.6630	0.5997
Total cover	*0.0001*	*0.0097*	*0.0336*	0.4752	*0.0834*	*0.0002*	0.3321	0.5933	*0.0569*	0.8428	*0.0116*	0.8607	0.7564	0.1127	0.2558
Avg. decay class	*0.0047*	0.3716	*0.0755*	*0.0668*	0.1340	*0.0028*	0.7824	0.6651	0.8484	0.7128	0.2242	0.9339	0.9033	*0.0519*	0.7821
Available NO$_3^-$	0.6998	0.4940	0.5693	0.7239	0.8602	0.5516	0.5252	0.4827	0.5023	0.9020	0.4276	0.1082	0.5155	0.7372	0.1923
Available NH$_4^+$	*0.0160*	0.7000	0.4447	0.8814	0.9053	0.2020	0.9743	0.7009	*0.0441*	0.2192	*0.0015*	*0.0051*	0.2794	*0.0821*	0.1010
Available PO$_4^{3+}$	*0.0331*	0.1973	0.5538	0.7673	0.5176	0.1960	0.7851	0.9701	0.1066	0.9894	*0.0594*	*0.0309*	0.3855	*0.0344*	0.9749
Decomposition rate	*0.0001*	0.6211	0.5819	0.4346	0.5396	*0.0001*	0.8452	0.8447	0.9815	0.4314	*0.0001*	0.5648	0.6077	0.3869	0.6282

Table 3-3. Discriminant function analysis of environmental variables examines differences among treatments for each forest type, showing standardized canonical discriminant functions for the different variables. Values in brackets are eigenvalues of the function, indicating variance among treatments accounted for by each function. Variables are ordered by absolute size of correlation within function, with larger values indicating greater importance in explaining treatment differences. Non-bold variables were of negligible importance in discriminating treatments and were not used in the stepwise analysis. Success rate of cross-validation, where each plot is classified into treatments based on functions derived from all other plots, is shown in italics. Higher percentages indicate that variables can successfully be used to classify

Deciduous dominated

Function	1 (0.542)
Litter type	**1.000**
Average # of CWM pieces	0.428
Average CWM diameter	0.218
Average CWM decay class	0.190
Available NO_3^-	0.155
CWM percent cover	0.136
Soil temperature – 30 cm	-0.062
Soil temperature – 10 cm	-0.051
Available NH_4^+	-0.044
Decomposition rate	0.029
Available PO_4^{3+}	-0.019
Soil moisture	-0.005

Cross-validation success= 50.0%

Mixedwood

Function	1 (0.643)
Litter type	**1.000**
Available PO_4^{3+}	0.148
Average # of CWM pieces	-0.144
CWM percent cover	-0.134
Average CWM diameter	-0.126
Average CWM decay class	-0.125
Soil temperature – 30 cm	0.101
Decomposition rate	-0.085
Soil moisture	0.047
Available NO_3^-	0.033
Available NH_4^+	0.022
Soil temperature – 10 cm	-0.003

Cross-validation success= 48.5%

Conifer dominated

Function	1 (0.369)
Litter type	**1.000**
Average # of CWM pieces	0.227
Available PO_4^{3+}	0.191
Soil temperature – 10 cm	0.112
Average CWM diameter	0.109
Available NH_4^+	-0.087
Average CWM decay class	0.087
CWM percent cover	0.061
Available NO_3^-	0.058
Decomposition rate	0.054
Soil temperature – 30 cm	0.049
Soil moisture	0.048

Cross-validation success= 40.4%

Table 3-4. Repeated measures analysis of variance comparing pre and post harvest per plot species diversity and percent cover within each forest type. Significant adjusted Pr > F values (p≤0.10) indicate significant variance over time (time), over time among treatments (time*treatment) and among treatments within each year (treat). Italicized values are considered significant. To avoid pseudoreplication, the 8 per plot values per compartment were averaged prior to analysis.

	Deciduous dominated					Mixedwood					Conifer dominated				
	Time	Time* Treat	Treat Pre	Treat Post 1	Treat Post2	Time	Time* Treat	Treat Pre	Treat Post 1	Treat Post2	Time	Time* Treat	Treat Pre	Treat Post 1	Treat Post2
Numerator d.f.	2	6	3	3	3	2	6	3	3	3	2	6	3	3	3
Error d.f.	16			8		16			8		14			7	
Percent cover															
Herb	*0.0037*	0.5156	0.3711	0.3447	0.8883	*0.0006*	0.5278	0.5242	0.2503	0.1226	*0.0035*	0.7187	0.9579	*0.0232*	0.2836
Shrub	0.2459	*0.0469*	0.7515	*0.0513*	0.6734	0.3918	0.1569	0.3835	0.3042	0.4641	*0.0667*	0.8698	0.3391	0.1254	0.3444
Total	*0.0021*	*0.0265*	0.1646	*0.0110*	0.6709	*0.0056*	0.2493	0.4517	0.2794	*0.0834*	*0.0050*	0.7907	0.9395	*0.0730*	*0.0534*
Richness															
Herb	*0.0001*	0.1230	0.7958	0.6679	0.7489	*0.0037*	0.3155	0.4211	*0.0703*	*0.0310*	*0.0001*	*0.0100*	0.9989	*0.0348*	*0.0053*
Shrub	*0.0021*	*0.0191*	0.6197	0.3113	0.6887	0.1151	0.7321	0.7146	0.6803	0.9347	0.5549	0.2891	0.9259	0.5288	0.8657
Total	*0.0130*	0.2615	0.9233	0.6582	0.8005	*0.0217*	0.3897	0.3707	0.1173	*0.0924*	*0.0005*	*0.0128*	0.9938	0.1090	*0.0480*
Shannon-Weiner diversity															
Herb	0.0739	0.9898	0.8070	0.6944	0.5044	*0.0263*	0.2085	0.7980	0.2278	0.3708	*0.0249*	*0.0638*	0.6288	*0.0061*	0.2205
Shrub	0.8099	*0.0515*	0.6511	0.5072	0.1770	*0.0664*	0.7718	0.3974	0.4625	0.6468	0.6502	0.7052	0.9138	0.7850	0.8023
Total	0.3761	0.3551	0.9455	0.7837	0.4025	*0.0492*	0.4395	0.6424	0.3172	0.3211	*0.0329*	0.2233	0.7859	0.1978	0.3817
Simpson's diversity															
Herb	0.2460	0.9412	0.6789	0.6534	0.4736	*0.0065*	0.5026	0.9411	0.2178	0.8369	*0.0801*	0.4479	0.5953	0.1789	0.3083
Shrub	0.9931	0.4747	0.8233	0.6057	0.1668	0.4733	0.4442	*0.0839*	0.1911	0.1927	0.2177	0.8090	0.6781	0.7321	0.8999
Total	0.3037	0.2160	0.9416	0.7454	0.3955	*0.0065*	0.4096	0.7623	0.2150	0.6150	*0.0282*	0.4086	0.8098	0.3397	0.4321

Table 3-5. Repeated measures analysis of variance comparing pre and post harvest per compartment diversity indices. Significant adjusted Pr > F values (p≤0.05) indicate significant variance over time: overall (time), among forest types (time*type), among treatments (time*treatment) or whether differences among treatments over time are not parallel in all forest types (time*type*treatment). Italicized values are considered significant.

Error degrees of freedom = 48	Time	Time*type	Time*treatment	Time*type*treatment
Degrees of freedom	2	4	6	12
Richness				
Herb	*0.0001*	*0.0174*	*0.0084*	0.7588
Shrub	*0.0001*	*0.0025*	0.2700	0.2977
Total	*0.0001*	0.8231	*0.0235*	0.5367
Shannon-Weiner diversity				
Herb	*0.0009*	0.5188	0.3541	0.7122
Shrub	*0.0006*	*0.0083*	0.8206	0.5171
Total	*0.0282*	0.4255	*0.0032*	0.8680
Simpson's diversity				
Herb	*0.0099*	0.5237	0.5024	0.8104
Shrub	0.8692	0.1733	0.8893	0.6644
Total	*0.0147*	0.0628	0.5357	0.8529

Table 3-6. PROTEST random rotational fit analysis comparing matrices of DCCA plot scores within treatments over time. Values indicate probability of an equal or closer fit due to chance between the two data matrices (lower values = matrices are more similar).

	pre vs. post1	post1 vs. post2	pre vs. post2
Deciduous dominated			
Clearcut	0.0001	0.0035	0.1300
20% partial harvest	0.0017	0.0038	0.1243
75% partial harvest	0.0074	0.0268	0.0609
Control	0.0002	0.0001	0.0001
Mixedwood			
Clearcut	0.0002	0.2056	0.0741
20% partial harvest	0.0637	0.2787	0.0756
75% partial harvest	0.0768	0.0645	0.0553
Control	0.0001	0.0001	0.0001
Conifer dominated			
Clearcut	0.2317	0.1265	0.1661
20% partial harvest	0.0381	0.0001	0.0191
75% partial harvest	0.0195	0.0142	0.0329
Control	0.0001	0.0001	0.0001

Fig. 3-1 – Location of EMEND
study site

a) b)

90x60 residual

60x40 residual

15m leave strip

5 m machine corridor
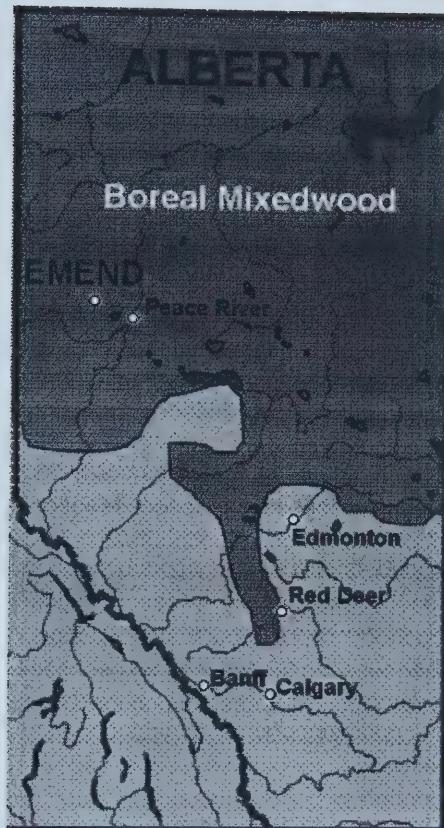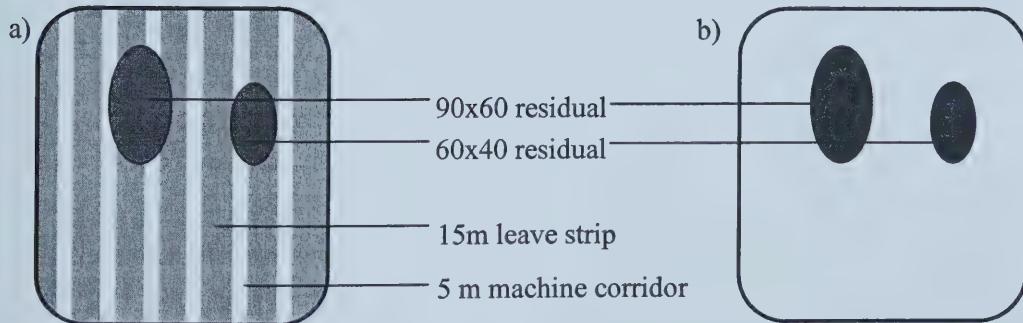
Fig. 3-2 – Harvesting design for compartments in the EMEND study site for a) partial harvest and b) clearcut
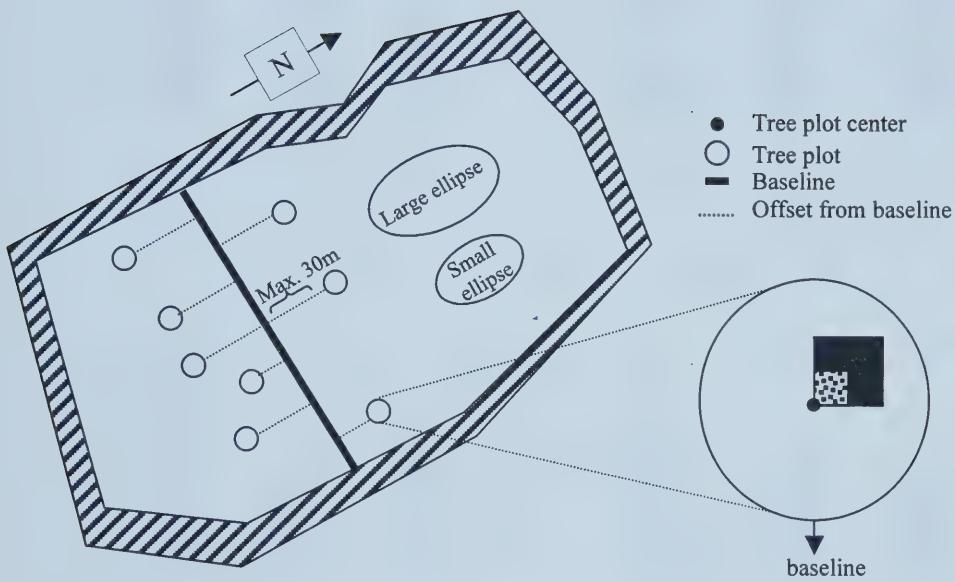
Figure 3-3. Layout of plots within each compartment (not to scale). Plots were offset from the existing baseline at distances selected from a random number table (<30 m). Magnified section shows a 1X1m herb plot (speckle) nested within a 2X2m shrub plot (black) within a 50m^2 circular tree plot. Striped area is a buffer (minimum 100m width).
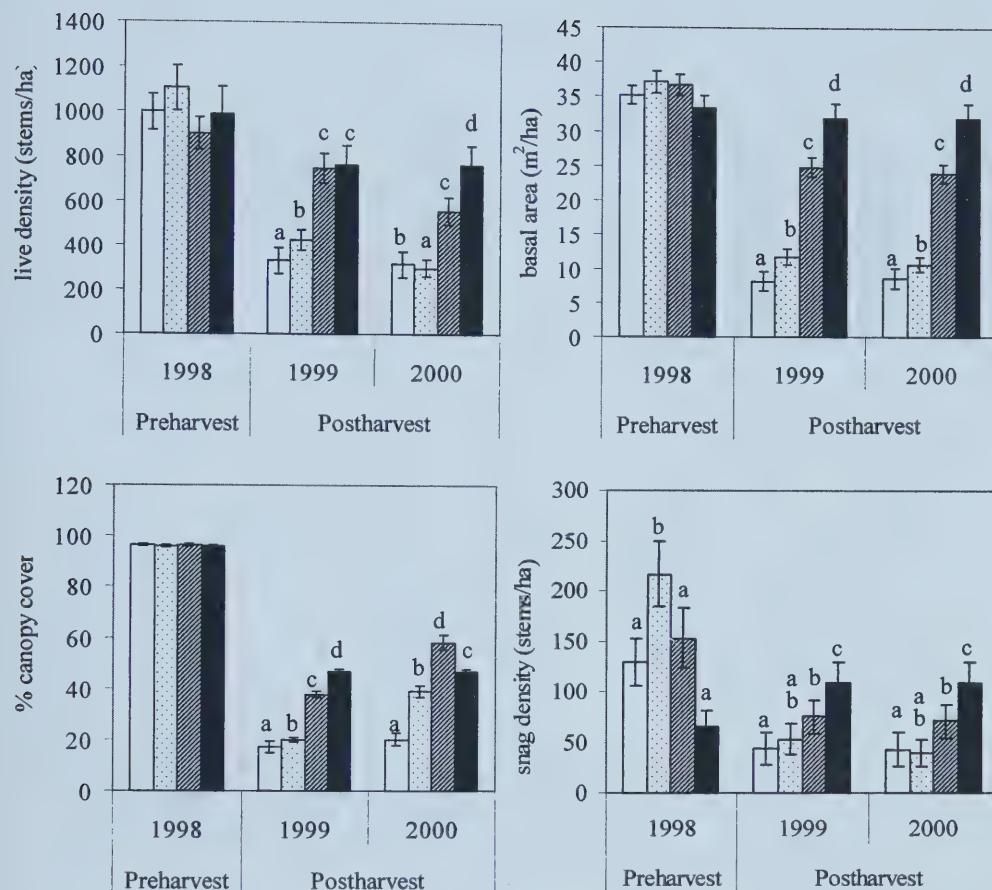
Figure 3-4. Canopy structure within harvest treatments (means ± s.e.) including clearcuts (white), 20% partial harvest (dots), 75% partial harvest (stripes) and control (black) across all forest types. Different letters indicate a significant difference between treatments within that year according to ANOVA least squared means comparison test (p≤0.05) Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 72 plots, controls ≈ 96 plots).
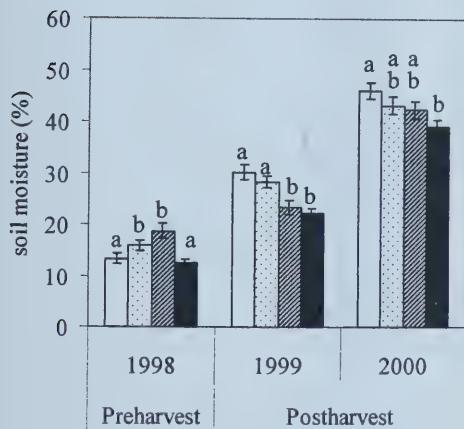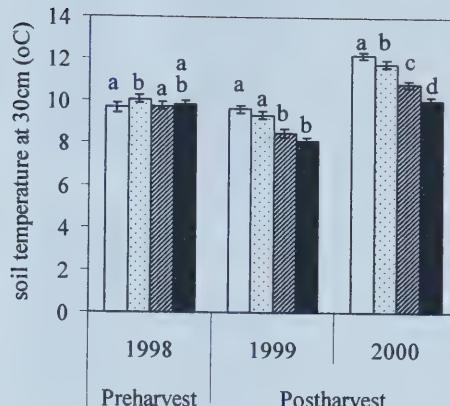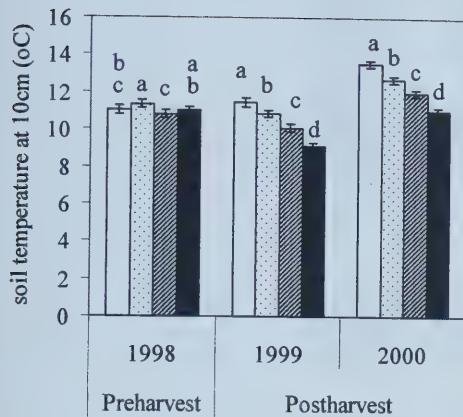
Figure 3-5. Soil temperature and moisture within harvesting treatments (means ± s.e.) for clearcuts (white), 20% partial harvest (dots), 75% partial harvest (stripes) and control (black) across all forest types. Different letters indicate a significant difference between treatments within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 72 plots, controls ≈ 96 plots).
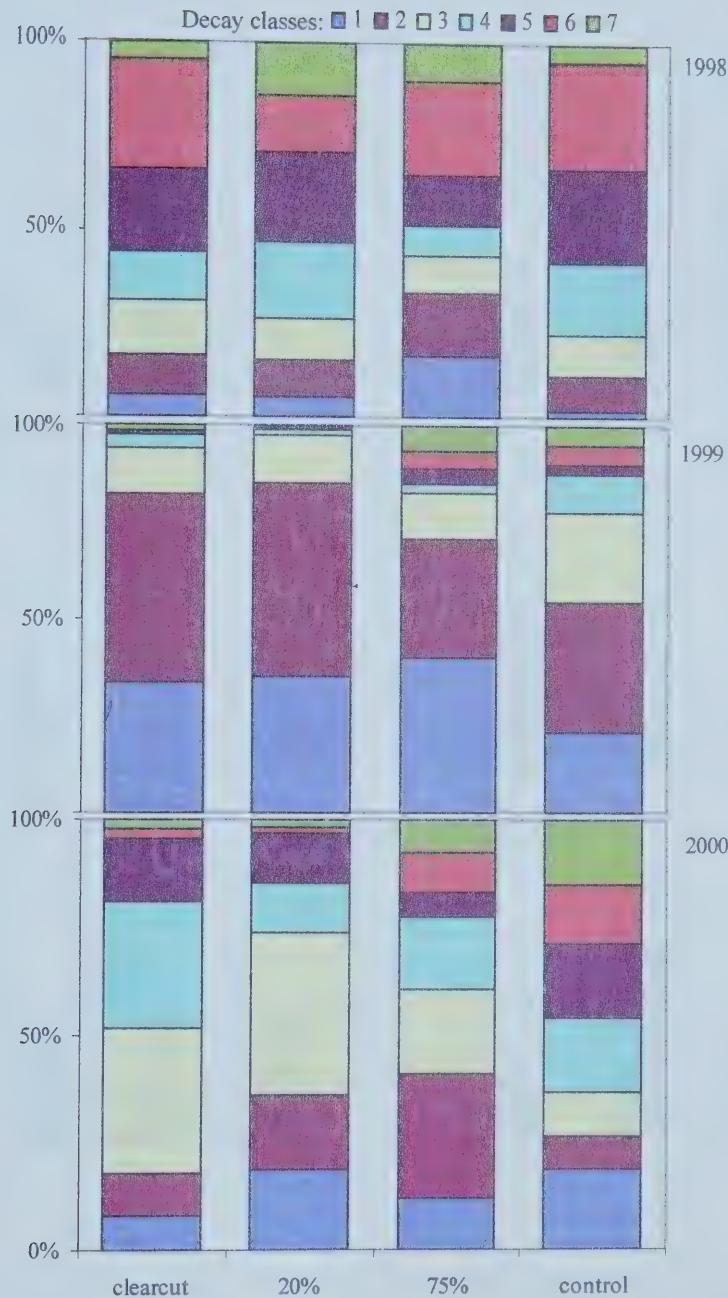
Figure 3-6. Decay class distribution of coarse woody material within treatments for all years (see Appendix for description of decay classes). All values are relative frequencies across all forest types.
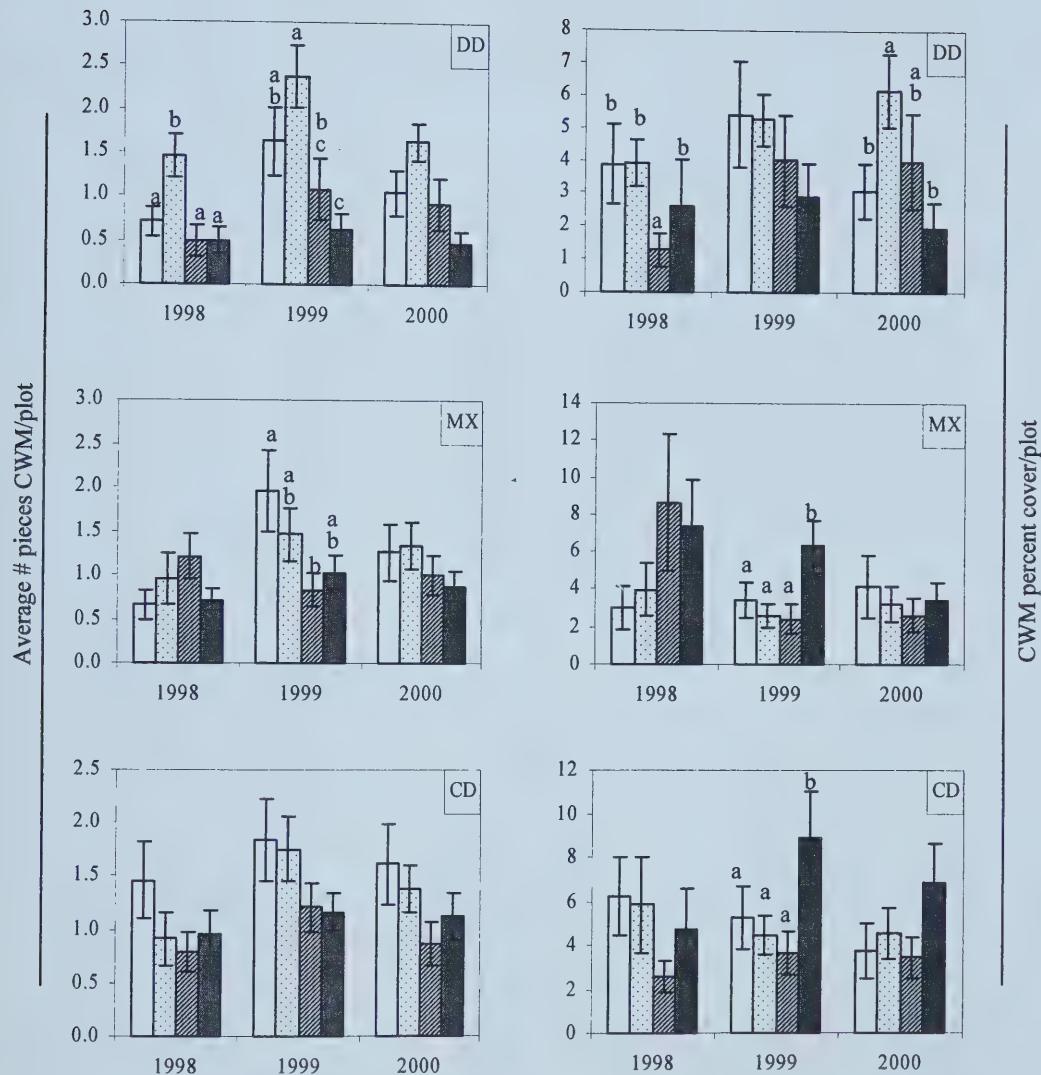
Figure 3-7. Coarse woody material (CWM) number of pieces and cover per plot within clearcut (white), 20% (dots) and 75% (stripes) partial harvest and control (black) treatments over time for each forest type (DD – deciduous dominated; MX – mixedwood; CD – conifer dominated). All values are means ± s.e. Different letters indicate significant difference between treatments within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment per forest type (clearcut, 20% and 75% ≈ 24 plots, controls ≈ 32 plots).
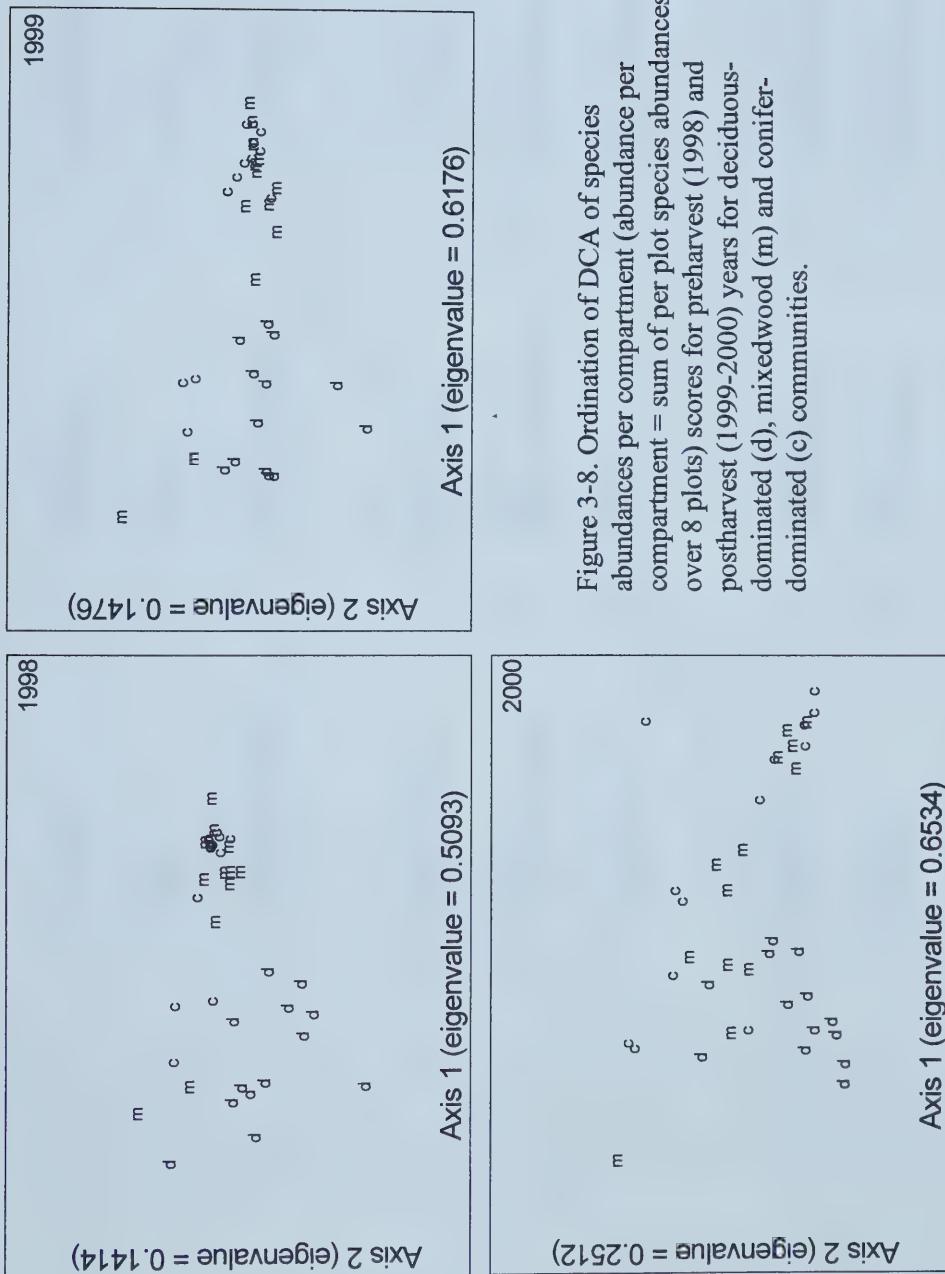
Figure 3-8. Ordination of DCA of species abundances per compartment (abundance per compartment = sum of per plot species abundances over 8 plots) scores for preharvest (1998) and postharvest (1999-2000) years for deciduous-dominated (d), mixedwood (m) and conifer-dominated (c) communities.
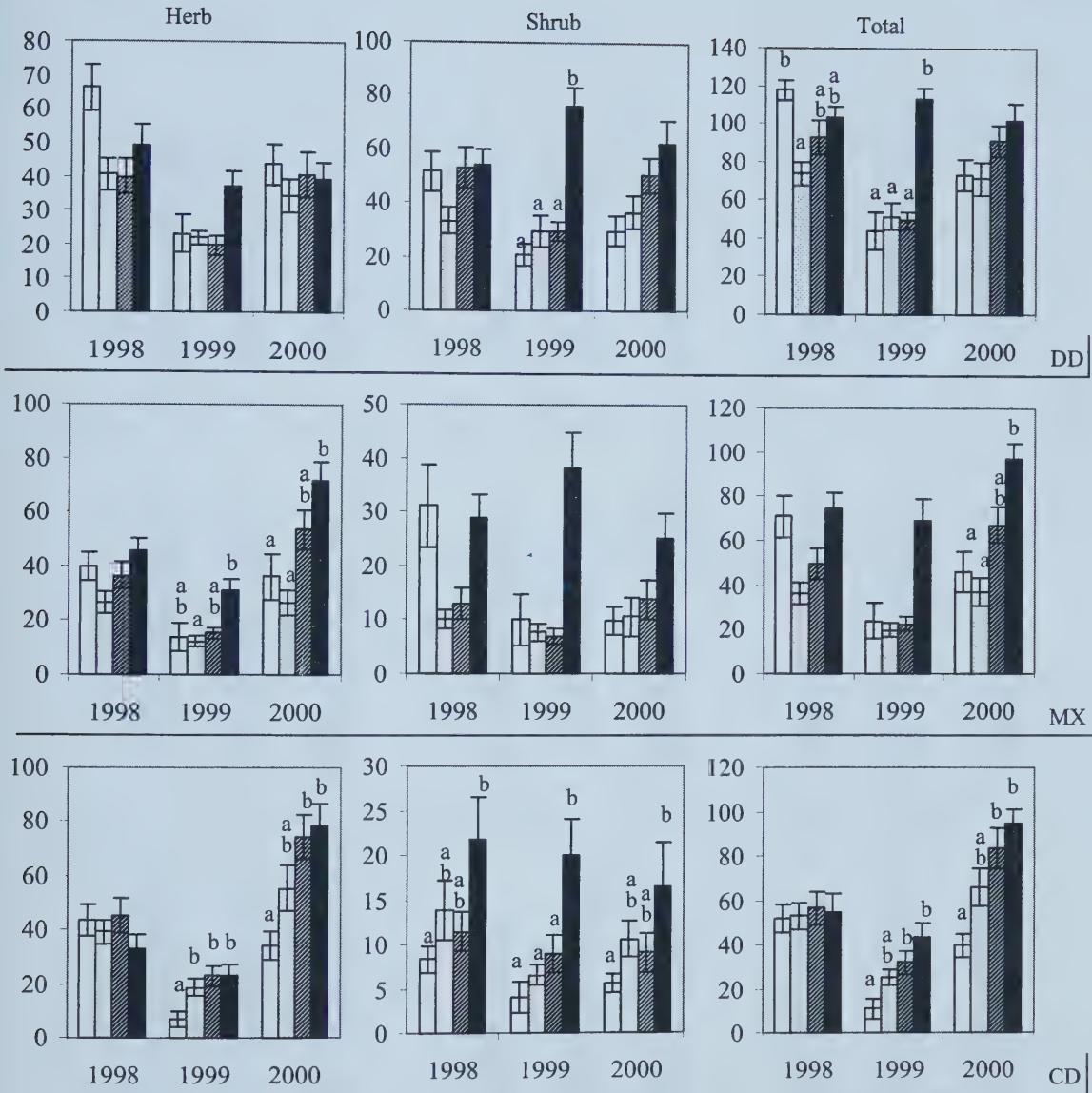
Figure 3-9. Percent cover of understory plants per plot (means ± s.e.) within each forest type (DD - deciduous dominated; MX-mixedwood; CD - conifer dominated) for clearcut (white), 20% (dots) and 75% (stripes) partial harvest, and control (black) treatments. Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 24 plots, controls ≈ 32 plots).
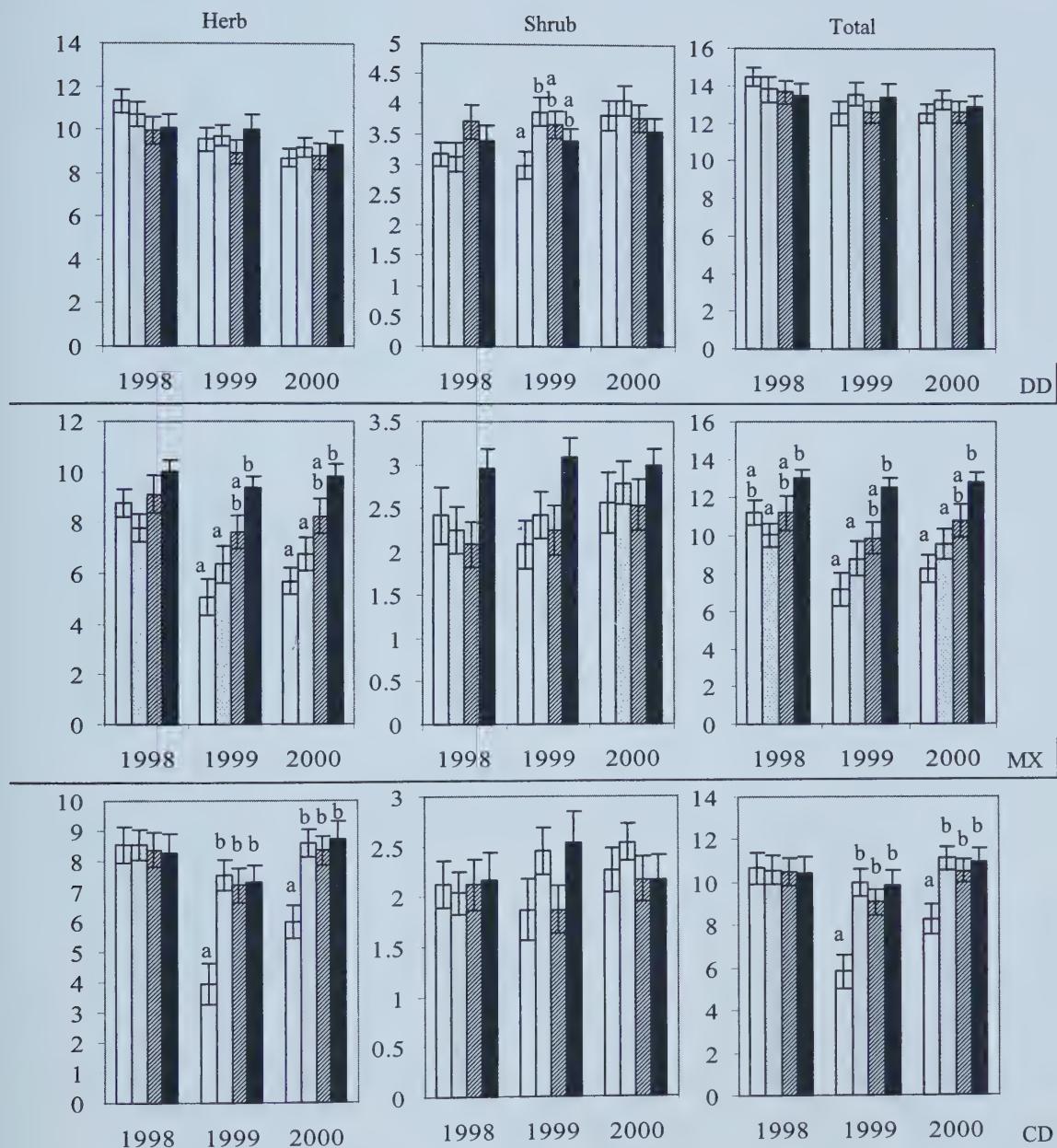
Figure 3-10. Richness (# of species) per plot within each forest type (DD - deciduous dominated; MX - mixedwood; CD - conifer dominated) for each harvest treatment including clearcut (white), 20% (dots) and 75% (stripes) partial harvest, and control (black) treatments (means ± s.e.). Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 24 plots, controls ≈ 32 plots).
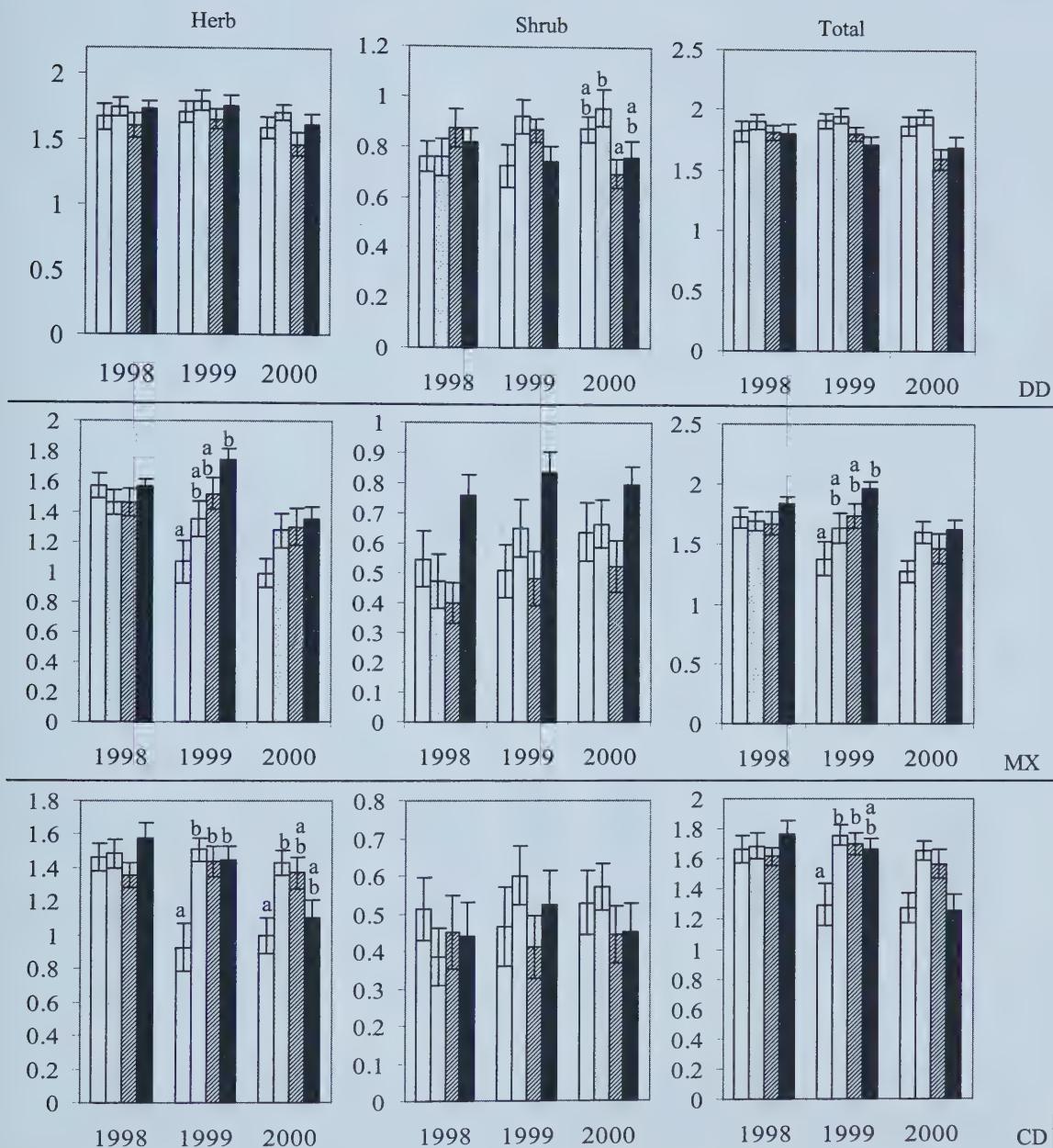
Figure 3-11. Shannon-Weiner diversity index per plot within each forest type (DD - deciduous dominated; MX-mixedwood; CD - conifer dominated) for each harvest treatment including clearcut (white), 20% (dots) and 75% (stripes) partial harvest, and control (black) treatments (means ± s.e.). Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 24 plots, controls ≈ 32 plots).

89
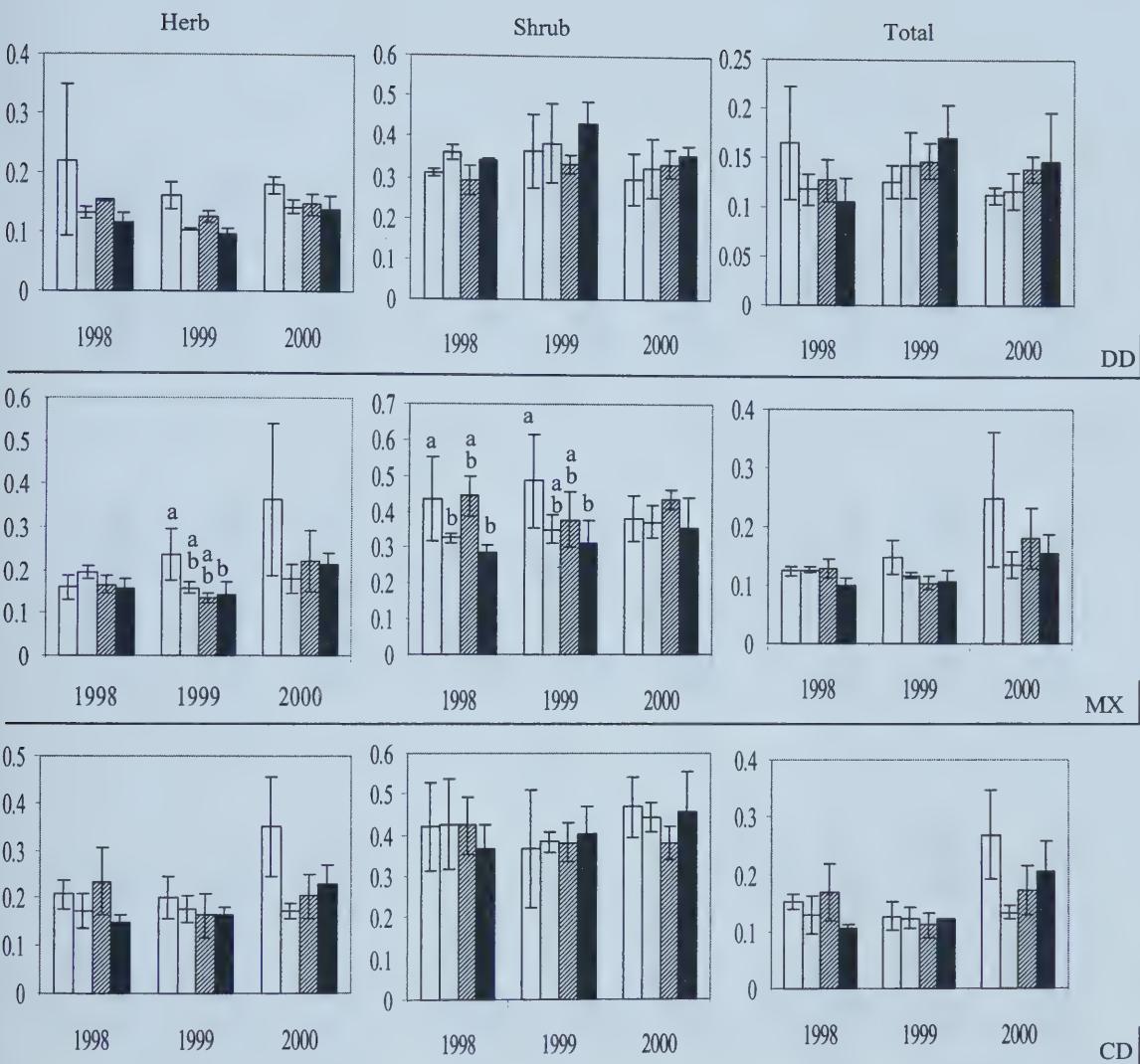
Figure 3-12. Simpson's diversity index per plot within each forest type (DD - deciduous dominated; MX -mixedwood; CD - conifer dominated) for each harvest treatment including clearcut (white), 20% (dots) and 75% (stripes) partial harvest, and control (black) treatments (means ± s.e.). Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all plots across the three stands per treatment in all forest types (clearcut, 20% and 75% ≈ 24 plots, controls ≈ 32 plots).

90
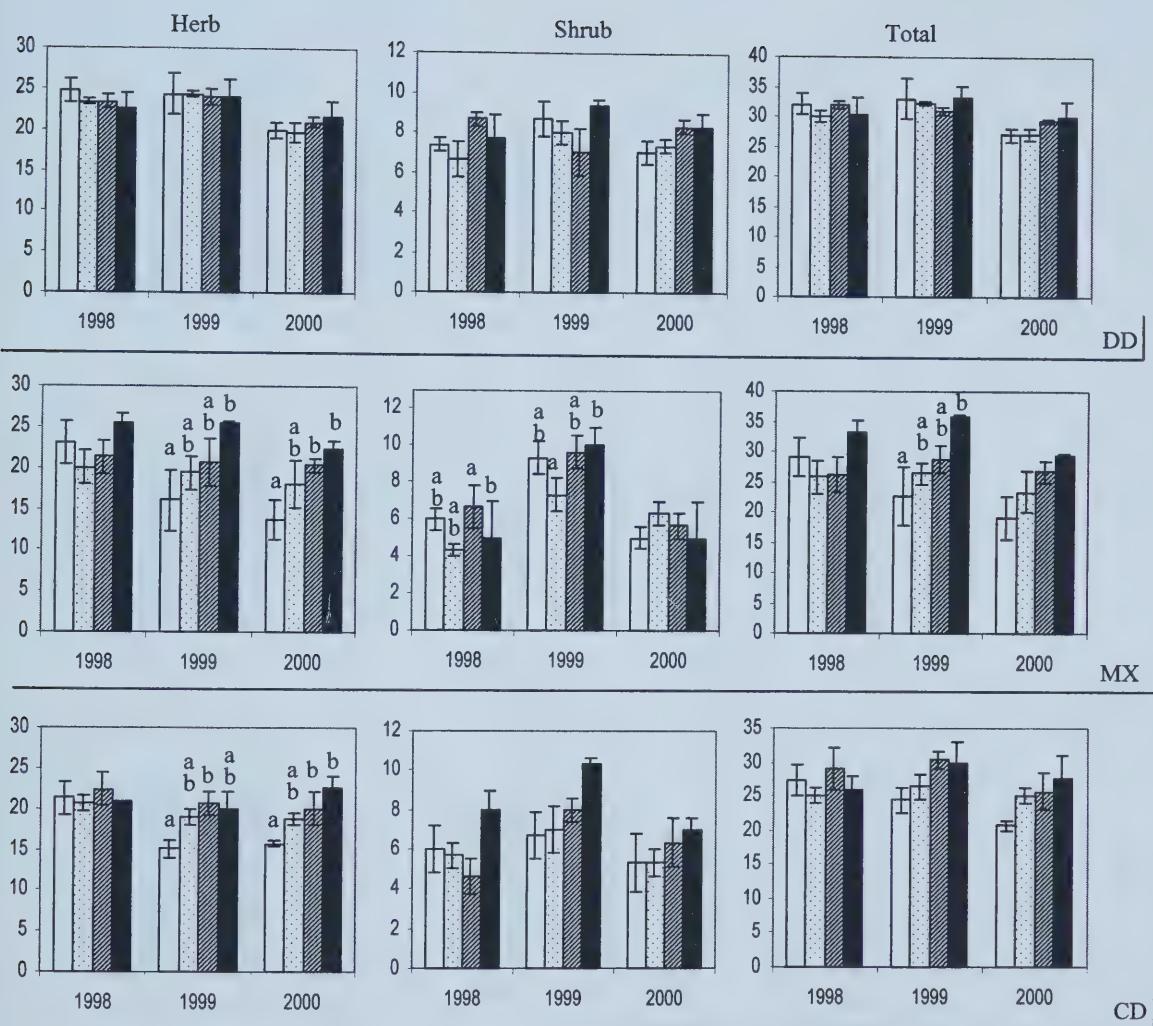
Figure 3-13. Richness (means ± s.e.) per compartment (calculated from total of species abundances over 8 plots) for each treament including clearcuts (white), 20% partial harvest (dots), 75% partial harvest (stripes) and control (black) within deciduous-dominated (DD), mixedwood (MX) and conifer-dominated (CD) forest types. Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all compartments across the three stands per treatment per forest type (clearcut, 20% and 75% ≈ 3 compartments, controls ≈ 4 compartments).
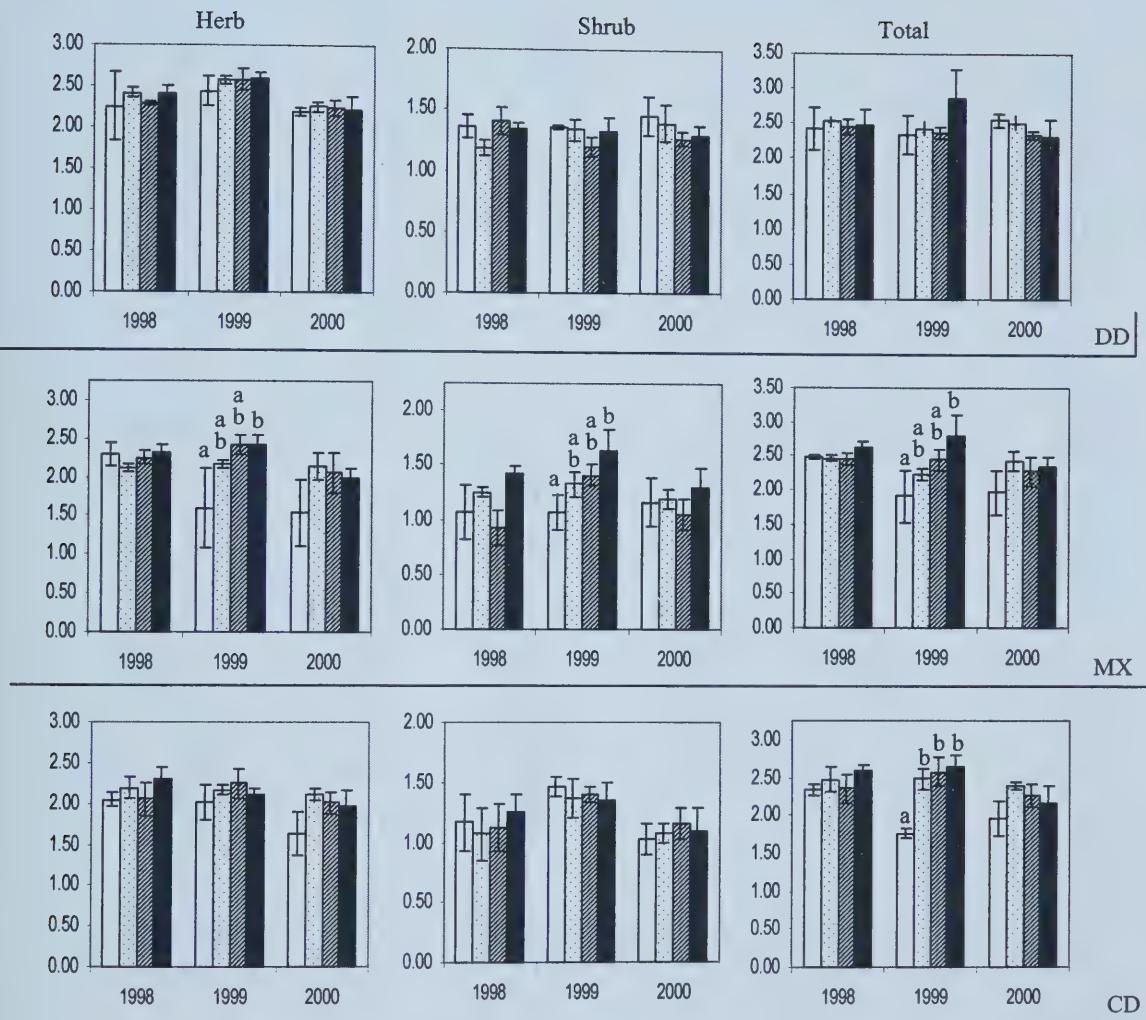
Figure 3-14. Shannon-Weiner diversity (means ± s.e.) per compartment (calculated from total of species abundances over 8 plots) for each treament including clearcuts (white), 20% partial harvest (dots), 75% partial harvest (stripes) and control (black) within deciduous-dominated (DD), mixedwood (MX) and conifer-dominated (CD) forest types. Those bars with different letters indicate significantly different values within that year according to ANOVA least squared means comparison test (p≤0.05). Each bar represents the mean (s.e.) of all compartments across the three stands per treatment per forest type (clearcut, 20% and 75% ≈ 3 compartments, controls ≈ 4 compartments).

92
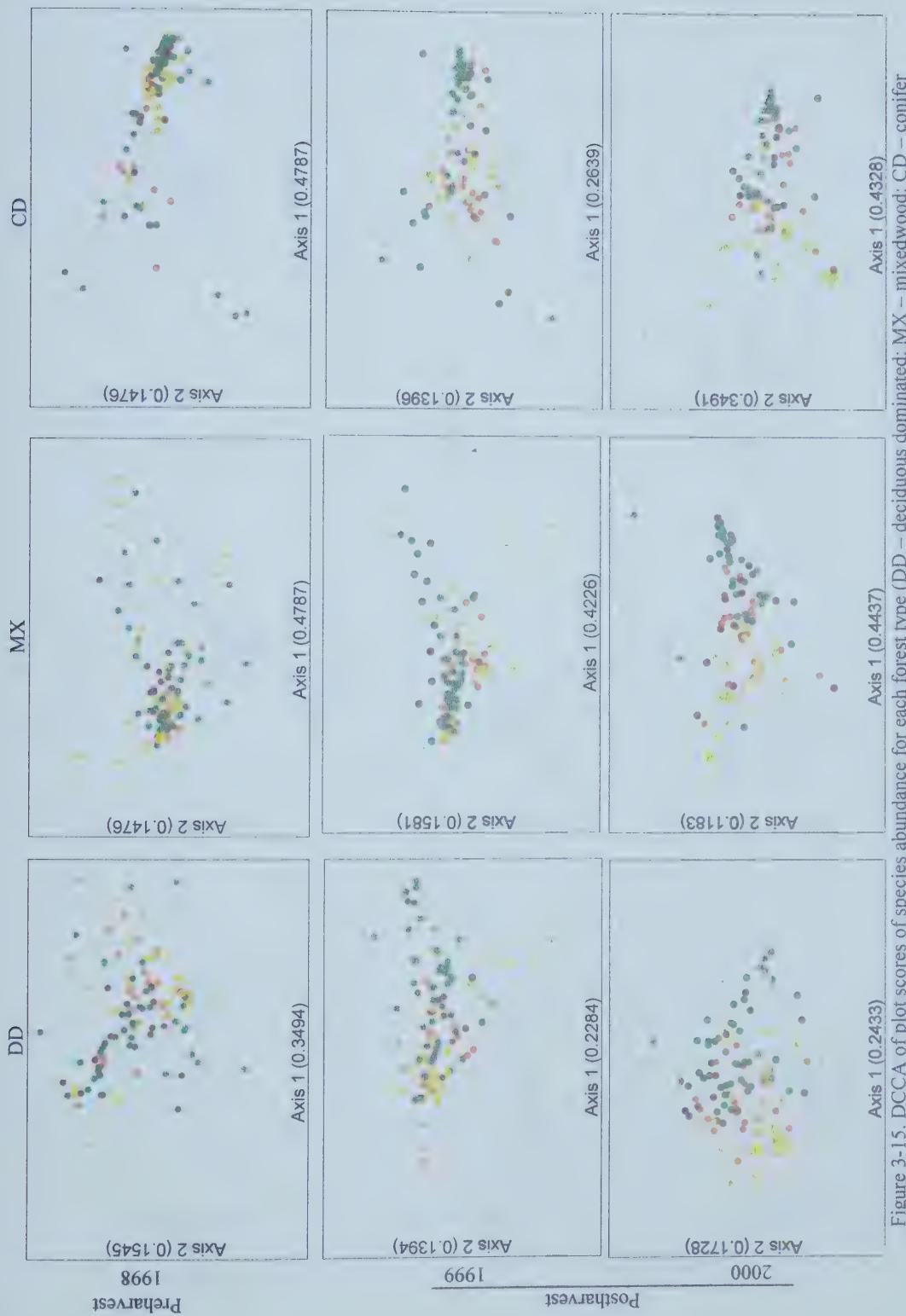
Figure 3-15. DCCA of plot scores of species abundance for each forest type (DD – deciduous dominated; MX – mixedwood; CD – conifer dominated) pre- and postharvest showing treatment species composition. Note segregation of treatments (yellow - clearcut; orange – 20% partial harvest; brown – 75% partial harvest; green – control) over time. Values in brackets are eigenvalues.
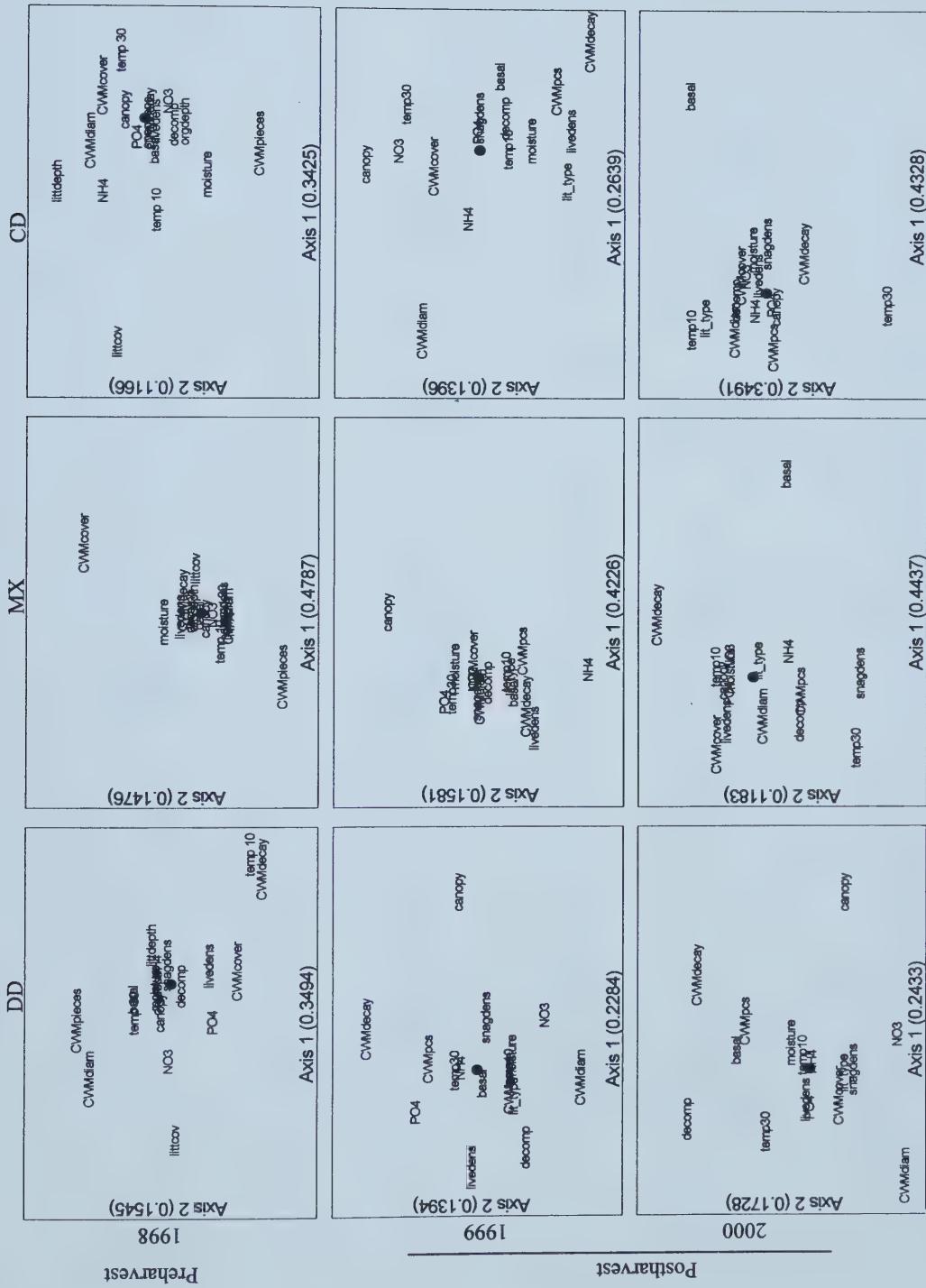
Figure 3-16. Ordination of canopy structure and environmental variables used to constrain axes of DCCA within each forest type (DD – deciduous dominated; MX – mixedwood; CD – conifer dominated). Those variables furthest from the zero correlation point (● = 0,0) are the most important factors within the axes. Values in brackets are eigenvalues.
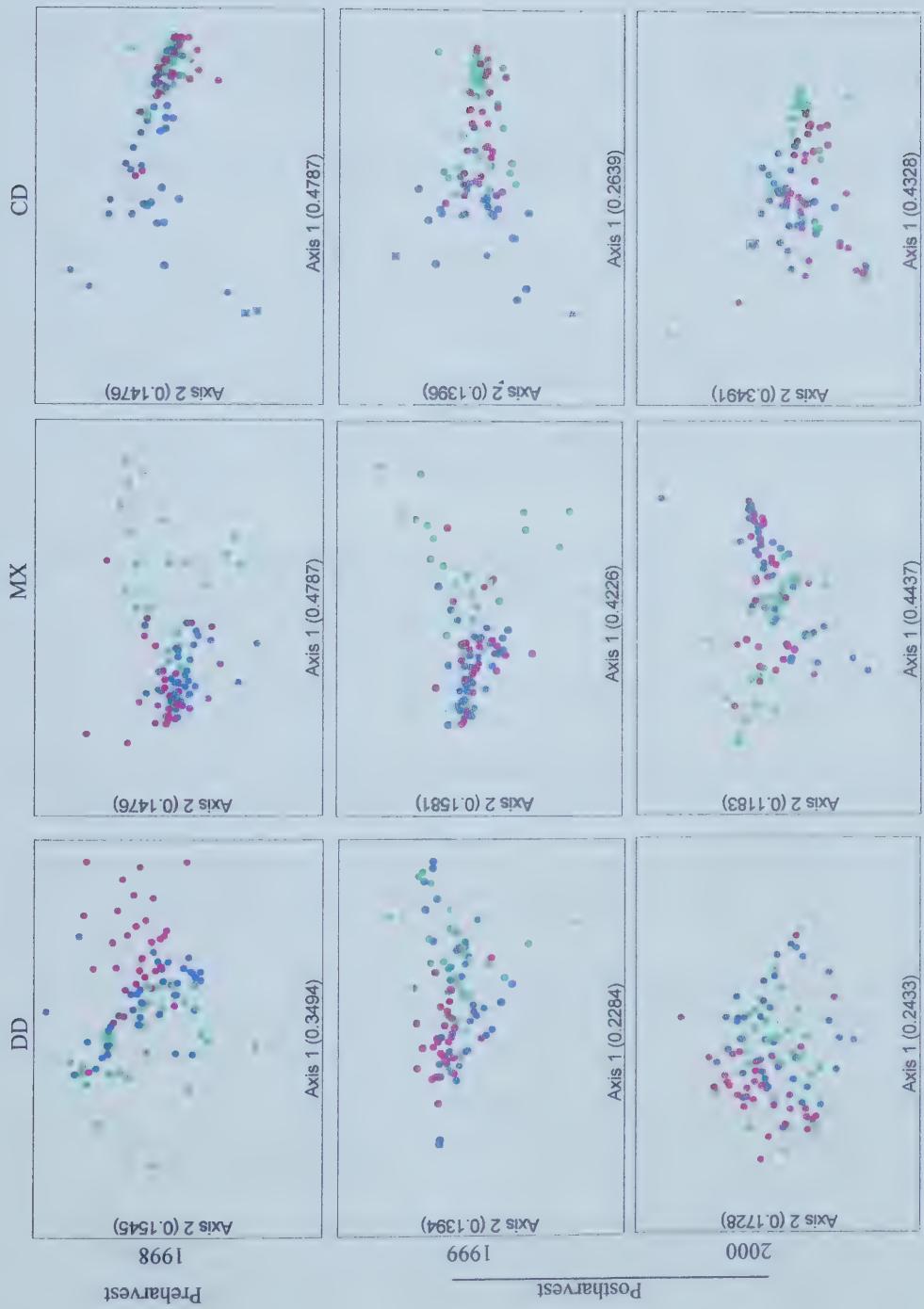
Figure 3-17. DCCA ordinations of plot scores showing stand understory species composition. Each colour represents one of three stands within each forest type (DD – deciduous dominated; MX – mixedwood; CD – conifer dominated). Note increased overlap (similarity) of stand species composition over time within forest types. Values in brackets are eigenvalues.

95

Bibliography

Alaback, Paul B. and F.R. Herman. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. Can. J. For. Res. 118: 1522-1530.

Barbour, M.G., Burk, J.H. & Wanna D. Pitts. 1987. Terrestrial Plant Ecology. Benjamin/Cummings Publishing Company: Don Mills, Ontario. 634 pp.

Beese, W.J. and Andrew A. Bryant. 1999. Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. For. Ecol. Manag. 115: 231-242.

Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79: 51-63.

Binkley, Dan. 1984. Ion exchange resin bags: Factors affecting estimates of nitrogen availability. Soil Sci. Soc. Am. J. 48: 1181-1184.

Bird G.A. and L. Chatarpaul. 1988. Effect of forest harvest on decomposition and colonization of maple leaf litter by soil microarthropods. Can. J. Soil Sci. 68: 29-40.

Black, R.A. & L.C. Bliss. 1978. Recovery sequence of Picea mariana - Vaccinium uliginosum forests after burning near Inuvik, Northwest Territories, Canada. Can. J. Bot. 56: 2020-2030.

Black, T.A., C.S. Tan & J.U. Nnyamah. 1980. Transpiration rate in Douglas fir trees in thinned and unthinned stands. Can. J. Soil Sci. 60:625-631.

Boyle, T.J.B. 1991. Biodiversity of Canadian forests: Current status and future challenges. Forestry Chronicle 68: 444-452.

Bréda, N., A. Granier and G. Aussenac. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiology. 15:295-306.

Carleton, T.J. & P. MacLellan. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience. 2: 141-152.

Carleton, T.J. & P.F. Maycock. 1980. Vegetation of the boreal forests south of James Bay: Non-centered component analysis of the vascular flora. Ecology. 61: 1199-1212.

Coates, K. Dave. 1997. Windthrow damage 2 years after parital cutting at the Date Creek silvicultural systems study in the interior cedar-hemlock forest of northwestern British Columbia. Can. J. For. Res. 27: 1695-1701.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science. 199: 1302-1310.

Connell, J.H. & R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. **Am. Nat. 111**: 1119-1144.

Constabel, A.J. & V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26: 1008-1014.

Cortina J. and V.R. Vallejo. 1994. Efects of clearfelling on forest floor accumulation and litter decomposition in a radiata pine plantation. For. Ecol. Manag. 70: 299-310.

Cumming, S.G., F.K.A. Schmiegelow and P.J. Burton. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. 10: 744-759.

DeGrandpré, Louis, D. Gagnon & Yves Bergeron. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. 4:803-801.

Egler, FE. 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. Vegetatio. 4: 412-418.

Foster, D.R. 1985. Vegetation development following fire in Picea mariana (black spruce) - Pleurozium forests of south-eastern Labrador, Canada. J. Ecol. 73: 517-534.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKie and Thomas Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In DA Perry, R Meurisse, B Thomas, R Miller, J Boyle, J Means, CR Perry and RF Powers (Eds.). Maintaining The Long-Term Productivity Of Pacific Northwest Forest Ecosystems. Timber Press, Portland, Oregon. pp. 82-97.

Franklin, S.F. 1998. Structural and functional diversity in temperate forests. In: Wilson, EO (Ed.), *Biodiversity*. National Academy Press, Washington DC, pp. 166-175.

Fredericksen, T.S., Brad D. Ross, W. Hoffman, M.L. Morrison, Jan Beyea, B.N. Johnson, M.B. Lester & Eric Ross. 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manag. 116: 129-139.

Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, J.S. Gerrow, G. Johnson & S. Woodley. 1996. Biodiversity implications of

changes in the quantity of dead organic matter in managed forests.
Environ. Rev. 4: 238-265.

Galindo-Leal, Carlos & Fred L. Bunnell. 1995. Ecosystem management:
Implications and opportunities of a new paradigm. For. Chron. 71: 601-606.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants
and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the
importance of the regeneration. Biol. Rev. 52: 107-145.

Haila, Yrjö. 1994. Preserving ecological diversity in boreal forests: ecological
background, research and management. Ann. Zool. Fennici 31: 203-217.

Halpern, Charles. 1988. Early successional pathways and the resistance and
resilience of forest communities. Ecology. 69: 1703-1715.

Hansen, A.J., T.A. Spies, F.J. Swanson and J.L. Ohmann. 1991. Conserving
biodiversity in managed forests. Bioscience 41: 382-392.

Harvey, B.D. and Yves Bergeron. 1989. Site patterns of natural regeneration
following clear-cutting in northwestern Quebec. Can. J. For. Res. 19: 1458-1469.

Hughes, J.W. and T.J. Fahey. 1991. Colonization dynamics of herbs and shrubs in
a disturbed northern hardwood forest. J. Ecol. 79: 605-616.

Jackson, Donald. 1994. PROTEST: A PROcrustean Randomization TEST of
community environment concordance. Ecoscience. 2: 297-303.

Jackson, S.M., Pinto, F., Malcolm, J.R. & E.R. Wilson. 2000. A comparison of pre-
European settlement (1857) and current (1981-1995) forest composition in
central Ontario. Can. J. For. Res. 30: 605-612.

Keenan, R.J. & J.P. Kimmins. 1993. The ecological effects of clearcutting. Environ.
Rev. 1: 121-144.

Kimmins, J.P. 1987. Forest Ecology. Macmillan: New York. 831 pp.

Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and
integrity. Forestry Chronicle 73: 229-232.

Landhausser, J. and V. Lieffers. 1997. Growth of Populus tremuloides in
association with Calamagrostis canadensis. Can. J. For. Res. 28: 396-401.

Lewin, R. 1986. Supply-side ecology. Science 234: 25-27.

Lieffers, V.C., C. Messier, K.J. Stadt, F. Gendron & P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

Lieffers, V.J. and K. Stadt. 1994. Growth of understory Picea glauca, Calamagrostis canadensis and Epilobium angustifolium in relation to overstory light transmission. Can. J. For. Res. 24: 1193-1198.

Messier, C., S. Parent and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9: 511-520.

Mladenoff, D.J., Mark A. White, John Pastor & Thomas R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecol. Appl. 3: 294-306.

Morris, Sherri Jeakins & R.E.J. Boerner. 1998. Interactive influences of silvicultural management and soil chemistry upon soil microbial abundance and nitrogen mineralization. For. Ecol. Manag. 103: 129-139.

Murdoch, W.W., Evans, F.C. & C.H. Peterson. 1972.Diversity and pattern in plants and insects. Ecology. 53: 819-828.

Navratil, S. 1995. Minimizing wind damage in alternative silvicultural systems in boreal mixedwoods. Canada Alberta Partnership Agreement in Forestry F042-91/124-1995E. Canadian Forest Service, Edmonton.

North, M., Chen, Jiquan, Smith, G., Krakowiak, L. & J. Franklin. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Sci. 70: 24-35.

Qi, Meiqin & J.B. Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Can. J. Bot. 76: 872-883.

Reader, R.J. & B.D. Bricker. 1992. Value of selectively cut deciduous forest for understory herb conservation: An experimental assessment. For. Ecol. Manag. 51: 317-327.

Riegel, G.M., R.F. Miller & William C. Krueger. 1992. Competition for resources between understory vegetation and overstory Pinus ponderosa in northeastern Oregon. Ecol. Appl. 2: 71-85.

Roberts, B.A., K.W. Deering & B.D. Titus. 1998. Effects of intensive harvesting on forest floor properties in Betula papyrifera stands in Newfoundland. J. Veg. Sci. 9: 521-528.

Roberts, M.R. and F.S. Gilliam. 1995a. Disturbance effects on herbaceous layer vegetation and soil nutrients in *Populus* forests of northern lower Michigan. J. Veg. Sci. 6: 903-912.

Roberts, M.R. and F.S. Gilliam. 1995b. Patterns and mechanisms of plant diversity in forested ecosystems: Implications for forest management. Ecol. Appl. 5: 969-977.

Ross, M.S., L.B. Flanagan & George H. LaRoi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Can. J. Bot. 64: 2792-2799.

Rubio, Agustín, Rosario Gavilán & Adrián Escudero. 1999. Are soil characteristics and understory composition controlled by forest management? For. Ecol. Manag. 113:191-200.

Schaefer, J.A. 1993. Spatial patterns in taiga plant communities following fire. Can. J. Bot. 71: 1568-1573.

Schimpf, David & Nicholas Danz. 1999. Light passage through leaf litter: Variation among northern hardwood trees. Ag. For. Meteorology. 97: 103-111.

Siitonen, Jaha, Petri Martikainen, Pekka Punttila and Josef Rauh. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manag. 128: 211-225.

Spies, T.A., William J. Ripple & G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4:555-568.

ter Braak, C.J.F. 1987a. CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. TNO Institue of Applied Computer Science. Wageningen.

ter Braak, C.J.F. 1987b. 5. Ordination. In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.) Data analysis in community and landscape ecology, pp. 91-173. Pudoc, Wageningen.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852

Vesterdal, Lars, M. Dalsgaard, C. Felby, Karsten Raulund-Rasmussen & Bruno Bilde Jørgensen. 1995. Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. For. Ecol. Manag. 77: 1-10.

Willson, M.F. & T.A. Comet. 1996. Bird communities of northern forests: Ecological correlates of diversity and abundance in the understory. Condor. 98: 350-362.

Yorks, Thad E. & Simon Dabydeen. 1999. Seasonal and successional understory vascular plant diversity in second-growth hardwood clearcuts of western Maryland, USA. For. Ecol. Manag. 119: 217-230.

Chapter 4: *General Discussion*

The boreal forest types studied did differ in environmental condition and understory species composition; in particular, the deciduous community differed substantially from the mixedwood and coniferous communities. Though some environmental factors were related to community composition, no environmental variables measured in this study were apparent drivers of understory community composition. Based on preharvest understory communities, and the responses of these forest types to harvesting treatments, it became apparent that forest types responded differently to disturbance, with deciduous communities exhibiting a lesser response than the other two types. These observed responses to disturbance, as well as the differing responses among forest types, were possibly linked to canopy related light regimes, as well as available reproductive propagules and prevailing edaphic conditions, and the effect of these factors on the regeneration niche.

Environmental response

Environmental variables varied with forest type, suggesting that some environmental factors are affected by canopy type. However, some factors varied within forest types among stands, indicating that some factors are independent of canopy, or at least have a wide range of variation within forest type.

Litter and CWM variables in this study differed among forest types preharvest, but also varied significantly among stands within a given forest type. Since these variables vary within a consistent canopy, it is unlikely that they are primary drivers in canopy composition. Moreover, since both factors are a product of overall stand community processes, they serve as an indicator of forest processes, not a cause of species distribution. The large amounts of litter in deciduous dominated forests are likely a result of seasonal foliage loss, as well as additional contribution of leaf litter by the extensive shrub layer. The differences in CWM cover and diameter were consistent with the assumption that conifer stands are later stages in succession; this assumption is also reflected in the

higher snag densities of the conifer stands. Older stands are likely to have more signs of past tree mortality (Freedman 1993, Freedman et al. 1996).

That these factors served as indicators was supported by postharvest results, wherein the litter and CWM levels associated with given stands did not remain static, but no new associations developed between harvesting treatments and litter and CWM variables. As an indicator of forest processes, these variables need time to respond to changes in those processes caused by harvesting. If they were important drivers of establishment, a pattern would likely have emerged at this early stage.

Soil temperature varied among forest types, where soil temperatures were higher under deciduous canopies. Soil temperature also varied with application of treatments, as did moisture, and varied in the same pattern for all forest types. The very direct relationship between canopy type and these variables would explain their strong correlation to harvesting level; increased light penetration with canopy removal caused increases in temperature, while lower tree densities decreased transpiration per unit area resulting in increased soil moisture. Based on these results, it is apparent that harvesting affects the forest environment, and that each harvesting type affects the environment differently. Therefore, different harvesting types produced different regeneration niches. This indicates different potentials for change in plant communities with different harvesting treatments. Based on the results of the discriminant function analysis, however, environmental variables could not be consistently used to classify the treatments; thus, it is less likely that plant community changes related to treatments were affected by changes in the environmental variables measured in this study.

It is important to note that environmental variables do not have a simple unidirectional relationship with the understory community. The environment is also affected by the understory, and not just vice versa. Understory cover, especially the shrub layer, also intercepts sunlight, which has important implications in light dynamics and the regeneration niche on the forest floor (Messier et al. 1998, Rowe 1955). In some studies, shrub species control of light

103

has been more highly correlated with herb community than has the canopy composition (Gilliam and Turrill 1993).

Plant community response

Understory plant communities were associated with specific forest types. However, while the mixedwood forest was predicted to be the most species diverse, this study found the deciduous community to have the highest understory diversity of the three types, with the highest amount of understory cover as well. The extensive shrub community associated with the deciduous community was the likely cause for its relatively high diversity. Dense shrub communities are often associated with deciduous forests, as a result of the higher subcanopy light levels found in these forests. Though there were substantial differences in the understory community diversity and composition among forest types, there were few species specifically associated with any one forest type. There was substantial overlap of composition among mixedwood and coniferous compartments in the DCA, though there were a few species specific to each of these forest types. This suggests that these specific species were present in abundances too small to substantially affect diversity measures, or that these different species were present in different forests in similar abundances. Since diversity indices only use abundance values, such differences in species composition would not affect diversity values.

Although understory communities did vary among forest types, there was also considerable variation both among stands of a given forest type and among plots within stands, a pattern which has been observed elsewhere (Sagers and Lyon 1997, Berger et al. 2000). Within each forest type, there was substantial variation in plant composition among all plots, but plot composition tended to be more similar among plots within the same stand. Since most canopy variables did not differ significantly among stands within each forest type, it can be assumed that these differences in understory species composition among stands were not driven solely by canopy structure (Qian et al. 1997, Pausas 1994, Sagers and Lyon 1997).

The deciduous community richness and diversity were significantly different than the coniferous and mixedwood communities, which suggested that this community could respond differently to disturbance than the other forest types. According to some studies, the high diversity of the deciduous community should have made it more stable following disturbance than the other community types (Connell 1978, Franklin et al. 1989), though this point has been disputed (eg. MacMahon 1980). In particular, since the deciduous community already experiences a wide range of environmental conditions due to seasonal loss of foliage, it may have a greater ability to remain stable following disturbance; such resistance is also known as inertia (Kimmins 1987).

Forest types did respond differently, with the deciduous community experiencing much smaller drops in diversity in the harvested treatments than the other communities, as had been found in other studies (Roberts and Gilliam 1995, Reader and Bricker 1992). This could be because of a smaller change in environmental conditions following harvesting in the deciduous community than in the mixedwood or coniferous communities. The similarity of light regime pre- and postharvest in the deciduous forest could be the main reason why the deciduous community changed less in response to harvesting.

In the mixedwood and coniferous forests, plot diversity decreased less with application of partial harvests compared to clearcuts, but all harvests still experienced some decrease in diversity, indicating a more substantial shift in regeneration niche than in the deciduous community. Compartment-level understory diversity, on the other hand, seemed fairly resilient after harvesting regardless of forest type. The lesser change in richness and SW alpha diversity in all forest types at the compartment (versus the plot) level suggests that while diversity changes may seem dramatic at the plot level, they actually have a much smaller effect on the overall species composition at larger spatial scales. It could be an example of how changes at some scales, if they cancel each other out in a mathematical calculation of a diversity index, may be masked in measurements taken at another scale.

The lesser response of diversity indices following partial harvesting (versus clearcutting) should not be adopted as evidence those communities are not changing pre- to postharvest. While diversity is maintained within the partial harvest treatments and even in the deciduous dominated clearcuts, this does not address invasion or disappearance of specific species or all changes in dominance and composition (Boyle 1991). The segregation of treatment DCCA plot scores indicated that while diversity was not changing substantially, the species composition was changing in the deciduous clearcuts, and in the partial harvests.

While changes occurred in species composition within each forest type with application of treatment, the plant community associated with the deciduous canopy stayed segregated from the other communities in DCA both before and after harvesting. Based on this alone, one might suppose that homogenization of forest types is not an issue in regards to harvesting. However, based on the response of plant communities within stands, homogenization is a concern. With the application of harvesting, the understory plant community composition became more homogeneous among stands of a given forest type. As such, the landscape mosaic of community types (forest type and associated understory) may be altered considerably.

Within each forest type, each stand possessed a different community composition of shrubs and herbs preharvest. Following harvesting, treatments became more different, while plot-level community composition among stands became more similar within each forest type. This suggests the possible creation of small fragments within compartments, consisting of similarly disturbed machine corridors and leave strips, which would result in a mosaic of much smaller pieces. Since samples were not taken specifically to compare these small fragments, no pattern appears to confirm this. Since these fragments are distributed throughout the larger treatment areas, any differences among these fragments may be masked within the greater pattern, similar to the way that differences among plot diversity measures are masked within compartment diversity measures. Alternatively, the mosaic may be rearranged so that areas of

106

treatment become new 'stands', while the original stand structure disappears, causing a redistribution of the mosaic.

Changes in the landscape following harvesting as elucidated above may lead to loss of a particular type of forest (Spies et al. 1994), an increase or decrease in the size of forest patches, or a change in the heterogeneity of forest types and patch sizes (Mladenoff et al. 1993). These are important components of biodiversity that some researchers say are as necessary to consider as species diversity (Boyle 1991, Galindo-Leal and Bunnell 1995, Kimmins 1997), in part because of their effect on resident wildlife (Hansen et al 1991, Haila 1994), especially those dependent on understory habitats, such as birds (Willson and Comet 1996) and phytophagous insects (Murdoch et al. 1992). All of these factors are components of ecosystem process, another aspect of forests that needs to be considered in preservation of biodiversity (Franklin 1998).

Relationship of environment and plant community

Environmental variables as indicators

As we have already discussed, some environmental variables are indicators of existing forest processes. It is likely that the correlations found between plant species composition and environmental variables were not evidence of environmental factors determining what community established, but were instead artifacts of what canopy type was present (Purdy, B.G., S.E. Macdonald and M.R.T. Dale, submitted to Silva Fennica). Quantity and quality of litter, CWM and snags can reveal past history of forest stand composition and mortality. As such, while they may have some small-scale effects on establishment of individual plants, they probably do not influence plant composition at the stand level. This is confirmed by DCCA; the relationship correlating CWM and litter patterns with plant composition preharvest disappeared once CWM and litter patterns were disrupted during harvesting, verifying that these variables do not predicate plant community patterns in the establishment phase. Over time, the correlation between these factors and

community may reappear once the community recovers, but they will always serve as indicators.

Effect of canopy on plant community composition

Canopy is an important variable in determining understory composition, as indicated by the difference in composition between the deciduous and other communities. Leaf area index has been shown to be very consistent across stands with similar canopy type, regardless of other environmental factors such as soil type (Messier et al. 1998); therefore, while it may vary substantially among forest types, it tends to be uniform within those communities. No environmental variable measured in this study showed a strong correlation with canopy that could explain why certain communities were associated with canopy type. This suggests light as a possible driver of community composition.

There is an acknowledged difference in light regime underneath conifer/mixedwood and deciduous canopies. The inherently higher levels of light found beneath a deciduous canopy provide an environment unique from that found under mixedwoods or coniferous canopies (Constabel and Lieffers 1996, Lieffers and Stadt 1994, Lieffers et al. 1999, Berger et al. 2000). In addition, mixedwood forests, though they contain deciduous trees, often experience below-canopy light levels similar to those below a pure conifer forest due to the angle of incidence of light in northern forests (Constabel and Lieffers 1996). This might explain the overlap of communities between mixedwood and conifer forest types. Once under- and overstory species establish in a stand, and the canopy species overtop the understory, the shading effect of that canopy may cause certain species to flourish or recede in numbers. Therefore, it is important to note that light must be considered as a factor controlling survival rather than establishment.

Another aspect of light dynamics that must be considered is the attenuation of light by understory layers. While this aspect of environment has been discussed briefly in the first section, its effect on composition of the understory community has not. In the deciduous community, the shrub

108

community was the only layer to show an increase in cover following harvesting. This is an excellent example of the interplay of multiple layers in light dynamics (Riegel et al. 1992). Shrubs are typically more plentiful under deciduous canopies than coniferous ones, and shrubs then contribute to light attenuation at the herb layer and ground levels (Constabel and Lieffers 1996, Messier et al. 1998). The tradeoff between these layers following harvesting may have maintained a fairly constant amount of light at ground level, thus keeping a stable light environment for the herb layer, and allowing it to remain unchanged (Gilliam and Turrill 1993).

Effect of canopy on plant community composition after harvesting

The DCAs showed that forest types still differed in their understory composition postharvest. This does not indicate that light levels were unaffected by harvesting, nor that light is not a controlling factor in understory composition. However, based on the following discussion, it does support the premise that light levels determine success of understory plants post-germination.

According to Grubb's regeneration niche theory (1977), a plant may only establish if a propagule is present, and if the niche is available in which to succeed. In this study, specific pools of propagules were available in each forest type, and even in each stand prior to disturbance. For the propagules from the predisturbance community to establish after harvesting, the correct niche had to be available for them to succeed. In the case of the deciduous community, the qualities of the niche important to the establishment of those propagules were not changed enough by harvesting to alter community diversity and composition. Because deciduous understory communities typically experience a higher ambient light level, and seasonal fluctuations in leaf cover (Constabel and Lieffers 1996, Ross et al. 1986), they have greater inertia, which enables them to persist relatively unchanged.

In the mixedwood and coniferous communities, the denser quality of spruce canopy may mean that the niche was changed more substantially by its removal. Light conditions vary beneath different types of canopy; light

attenuation is greater beneath a coniferous canopy than under a broadleaf canopy (Constabel and Lieffers 1996, Lieffers and Stadt 1994, Lieffers et al. 1999). Therefore, removal of canopy containing conifers is likely to precipitate a greater change in light conditions at ground level than removal of a deciduous one. As a result, even if propagules from the predisturbance community were to establish, their success rate may be different postharvest. This may explain why the DCCA in these communities explained a greater proportion of the variance among treatments.

Effect of edaphic condition and reproductive potential on plant communities

As mentioned previously, the existence of different understory communities associated with stands within a forest of relatively uniform light regime suggests that other factors also define the regeneration niches of understory species. The low eigenvalues of some of the postharvest DCCA ordinations, especially those in the deciduous community, as well as low discriminant function eigenvalues, indicate that other environmental factors that were not measured might yield a better account of variance within the species distribution.

It is possible that persistence of species within a given community after a disturbance event may be more dependent on a reproductive potential, such as seed banks (Lewin 1986, DeGrandpré et al 1993) *sensu* initial floristics theory (Egler 1954) or long-term prevailing edaphic conditions (Harvey et al. 1995), than the environment created by a given disturbance. In one study, results indicated that while understory composition was related to existing soil conditions and application of silviculture treatments, there was no apparent connection between silviculture treatments and soil conditions (Rubio et al. 1999). This simply indicates that the relationship may not be a simple linear process of treatment affecting environment which in turn affects vegetation.

While some studies suggest that previous presence/absence of a species is the strongest predictor of post-disturbance herbaceous community structure (Halpern 1988, Hughes and Fahey 1991), other studies suggest that the

coincidence of over and understory communities is primarily due to common site requirements (Carleton & Maycock 1980) not due to any effect of canopy on understory or vice versa. This may be an indication that reproductive potential in the form of viable seeds or rhizomes, as well as existing edaphic conditions, are more important determining factors than canopy removal or associated environmental changes in determining the post-disturbance community composition (Hughes and Fahey 1991, Keenan and Kimmins 1993). The lack of change in plant community diversity in the 20% and 75% harvests, as well as the overlap of these same treatments in DCCA could support this theory. Specifically, the restriction of machine traffic to corridors in the treatments applied in this study means that the level of ground disturbance is the same in both of these harvest regimes.

Based on the reduced impact of partial harvesting on canopy related, reproductive and edaphic factors that may affect the understory community, partial harvesting may be a useful alternative to clearcutting. This is reflected in the lesser effect of partial harvesting on diversity and richness values than that seen in clearcuts. Since soil disturbance is limited to ¼ of the land area harvested, shifts in community postdisturbance may be reduced. In addition, retention of canopy, especially in communities containing conifers in the canopy, could reduce shifts in the regeneration niche available to establishing plants, allowing communities to remain stable after disturbance.

Forest management implications

Since the boreal forest is a mosaic of different forest types composed of different stands, and a complex interplay of canopy, understory, light and other factors determine the structure of these stands, then a unique set of processes may be occurring within each stand. Maintaining the distribution and heterogeneity of these stands on the landscape is an important element of preserving biodiversity.

To achieve this, creating the appropriate regeneration niche at the moment of establishment is crucial. Because both canopy and understory

111

establish at this moment, it is not sufficient to provide the conditions hospitable to only some species. While some invasive species may intrude at early stages after disturbance, they will likely disappear over time. On the other hand, species that disappear after harvesting will likely not reappear over time. Shading of the canopy may eventually determine which species will succeed in the long term, but it is vital to remember that the forests have a multilayer structure. Shrubs may establish concurrently with and independent of the canopy, potentially affecting canopy growth and creating a complex light regime that is not consistent throughout a given forest type; therefore, the final community composition is not solely a product of the canopy.

Since forest types possess these complex plant/environment relations, removing part of or the entire canopy in a forest may affect future understory composition differently from stand to stand. A difference in amount or type of canopy cover may affect the success of understory species beneath it. However, since the establishment of canopy and understory occur at the same time, there is no guarantee that the regrowth of the same canopy type on a given site is going to yield the same understory (Carleton and Maycock 1980). Other drivers, such as seed availability, may be more important at the establishment stage in assuring the return of a similar understory community (Hughes and Fahey 1991, Lewin 1986, Halpern 1988).

Moreover, the differences among forest types suggest that different management approaches should be taken for each. Due to the greater changes in light regime, forests containing conifers respond more dramatically to canopy removal, even in partial harvests. Due to the denser quality of coniferous canopy, it may exert a more limiting effect on the understory: therefore, the understory may experience a more substantial change in regeneration niche postharvest and thus be more prone to change following harvesting. This being the case, those stands that have previously contained conifers may benefit more from partial harvesting. Maintaining a partial canopy to provide some shade did lessen changes in the understory plant community compared to clearcutting in mixedwood and coniferous stands.

Feasibility of partial harvesting

Immediately following harvesting, measures of canopy cover, basal area and live density verified that the partial harvesting treatments were applied as intended; however, blowdown proved to be a major concern in the feasibility of the strip harvesting process. The exposure of trees that have not been wind-hardened to substantial wind force is an acknowledged weak point of partial harvesting techniques (Coates 1997).

Regardless of the cause, the loss of residual canopy, especially in the 20% treatment, may mean that the complex and more labour intensive harvesting pattern might not be considered worthwhile unless the short-term retention of canopy, or the CWM resulting from the blowdown, has a significant benefit on the long-term community structure. Based on the results of this study, there is a value, especially in the forest types with conifers in the canopy, in retaining some shading canopy.

Implications for succession

Recent studies propose that aspen-dominated communities may not be an early successional stage preceding a mixedwood or coniferous community as previously suggested, but are instead a unique successional pathway (Cumming et al. 2000, Bergeron and Dubuc 1989). This supports recent suggestions that harvesting methods that intend to mimic natural disturbance should consider not just a pattern of disturbance, but should instead incorporate the unique successional patterns and processes of each community on a site-specific basis (Roberts and Gilliam 1995b, Galindo-Leal and Bunnell 1995) with attention given to determining patterns of natural variation (Haila 1994). While this study does not confirm the long-term successional patterns of the site, results suggest that the establishment and success of understory species after partial and total canopy harvesting may be different in different community types, emphasizing a need to approach harvesting in each community with respect for its unique properties and processes.

Suggestions for future research

While the results of this study indicate that light is an important factor in environment/vegetation dynamics, no direct light measures were taken. A study at the EMEND site that incorporated direct light measurement under the canopy and understory layers could shed additional light on these dynamics. In fact, Lieffers et al. (1998) suggest that more studies of this type incorporate light measures of this type. Moreover, a study of the reproductive potential (including viable seed banks, rhizomes and other reproductive organs) of the disturbed vs. undisturbed areas, as well as the deciduous vs. the mixedwood and conifer communities, would also be useful on confirming the relationships postulated in this study. Of course, the short-term results of this study cannot predict what the mature forest will look like; to extend this study indefinitely would provide valuable information about the long-term impacts of this type of harvesting.

Additional work could be done comparing the changes in the partial harvest community to those found following fire of different intensities. Since these results suggest that partial harvests may be a way to capitalize on the inertia of forest communities, it would be interesting to compare this method with low intensity fires that allow substantial canopy survival and do not return succession to its early stages. This would be a shift from the bulk of studies to date comparing natural and human disturbance, which have mainly focused on more catastrophic disturbances.

Bibliography

Berger, Alaina L. and Klaus J. Puettmann. 2000. Overstory composition and stand structure influencing herbaceous plant diversity in the mixed aspen forest of northern Minnesota. Am. Midl. Nat. 143: 111-125.

Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79: 51-63.

Boyle, T.J.B. 1991. Biodiversity of Canadian forests: Current status and future challenges. Forestry Chronicle 68: 444-452.

Carleton, T.J. & P.F. Maycock. 1980. Vegetation of the boreal forests south of James Bay: Non-centered component analysis of the vascular flora. Ecology. 61: 1199-1212.

Coates, K. D. 1997. Windthrow damage 2 years after parital cutting at the Date Creek silvicultural systems study in the interior cedar-hemlock forest of northwestern British Columbia. Can. J. For. Res. 27: 1695-1701.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science. 199: 1302-1310.

Constabel, A.J. & V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. 26: 1008-1014.

Cumming, S.G., F.K.A. Schmiegelow and P.J. Burton. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. 10: 744-759.

DeGrandpré, Louis, D. Gagnon & Yves Bergeron. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. 4:803-801.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. Vegetatio. 4: 412-418.

Franklin, J.F. 1998. Structural and functional diversity in temperate forests. In: Wilson, EO (Ed.), *Biodiversity*. National Academy Press, Washington DC, pp. 166-175.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKie and Thomas Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In DA Perry, R Meurisse, B Thomas, R Miller, J Boyle, J Means, CR Perry and RF Powers (Eds.). Maintaining The Long-Term Productivity Of Pacific Northwest Forest Ecosystems. Timber Press, Portland, Oregon. pp. 82-97.

Freedman, B. 1993. Old-growth forests and ecologically sustainable forestry. *In* Forestry on the hill. Old growth forests. Canadian Forestry Association, Ottawa, Ont. pp. 29-32.

Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, J.S. Gerrow, G. Johnson & S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4: 238-265.

Galindo-Leal, Carlos & Fred L. Bunnell. 1995. Ecosystem management: Implications and opportunities of a new paradigm. For. Chron. 71: 601-606.

Gilliam, F.S. and N.L. Turrill. 1993. Herbaceous layer coer and biomass in a young vs. a mature stand of a coastal Appalachian hardwood forest. Bull. Torrey Bot. Club. 120: 445-450.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration. Biol. Rev. 52: 107-145.

Haila, Yrjö. 1994. Preserving ecological diversity in boreal forests: ecological background, research and management. Ann. Zool. Fennici 31: 203-217.

Halpern, Charles. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology. 69: 1703-1715.

Hansen, A.J., T.A. Spies, F.J. Swanson and J.L. Ohmann. 1991. Conserving biodiversity in managed forests. Bioscience 41: 382-392.

Harvey, B.D., Leduc, Alain & Yves Bergeron. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. Can. J. For. Res. 25: 1658-1672.

Hughes, J.W. and T.J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. J. Ecol. 79: 605-616.

Keenan, R.J. & J.P. Kimmins. 1993. The ecological effects of clearcutting. Environ. Rev. 1: 121-144.

Kimmins, J.P. 1987. Forest Ecology. Macmillan: New York. 831 pp.

Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and integrity. Forestry Chronicle 73: 229-232.

Lewin, R. 1986. Supply-side ecology. Science 234: 25-27.

Lieffers, V.C., C. Messier, K.J. Stadt, F. Gendron & P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

116

Lieffers, V.J. and K. Stadt. 1994. Growth of understory Picea glauca, Calamagrostis canadensis and Epilobium angustifolium in relation to overstory light transmission. Can. J. For. Res. 24: 1193-1198.

MacMahon, J.A. 1980. Ecosystems over time: succession and other types of change. In RH Waring (Ed.) Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Cornwallis, Oregon. pp. 27-58.

Messier, C., S. Parent and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9: 511-520.

Mladenoff, D.J., Mark A. White, John Pastor & Thomas R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecol. Appl. 3: 294-306.

Murdoch, W.W., Evans, F.C. & C.H. Peterson. 1972.Diversity and pattern in plants and insects. Ecology. 53: 819-828.

Pausas, J.G. 1994. Species richness patterns in the understory of Pyrenean *Pinus sylvestris* forest. J. Veg. Sci. 5: 517-524.

Qian, Hong, Karel Klinka & Bela Sivak. 1997. Diversity of the understory vascular vegetation in 40 year-old and old-growth forest stands on Vancouver Island, British Columbia. J. Veg. Sci. 8: 773-780.

Reader, R.J. & B.D. Bricker. 1992. Value of selectively cut deciduous forest for understory herb conservation: An experimental assessment. For. Ecol. Manag. 51: 317-327.

Riegel, G.M., R.F. Miller & William C. Krueger. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. Ecol. Appl. 2: 71-85.

Roberts, M.R. and F.S. Gilliam. 1995. Disturbance effects on herbaceous layer vegetation and soil nutrients in Populus forests of northern lower Michigan. J. Veg. Sci. 6: 903-912.

Ross, M.S., L.B. Flanagan & George H. LaRoi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Can. J. Bot. 64: 2792-2799.

Rowe, J.S . 1955. Uses of undergrowth plant species in forestry. Ecology. 37: 461-473.

Rubio, Agustín, Rosario Gavilán & Adrián Escudero. 1999. Are soil characteristics and understory composition controlled by forest management? For. Ecol. Manag. 113:191-200.

Sagers, C.L. and Jonathon Lyon. 1997. Gradient analysis in a riparian landscape: contrasts among forest layers. For. Ecol. Manag. 96: 13-26.

Spies, T.A., William J. Ripple & G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4:555-568.

Willson, M.F. & T.A. Comet. 1996. Bird communities of northern forests: Ecological correlates of diversity and abundance in the understory. Condor. 98: 350-362.

Appendices

Appendix 1. Plot locations

Compartment	Treatment	Forest type	Plot #	Base line	Baseline increment	Distance from baseline
850	clearcut	adom	1	A3	20m	7m N
850	clearcut	adom	2	A3	40m	8m S
850	clearcut	adom	3	A3	40m	21m S
850	clearcut	adom	4	A3	60m	3m S
850	clearcut	adom	5	A3	60m	25m S
850	clearcut	adom	6	A3	80m	6m N
850	clearcut	adom	7	A3	80m	7m S
850	clearcut	adom	8	A3	80m	27m S
851	0.7	adom	1	A4	60m	28m N
851	0.7	adom	2	A4	60m	20m S
851	0.7	adom	3	A4	80m	20m S
851	0.7	adom	4	A4	100m	25m N
851	0.7	adom	5	A4	120m	29m N
851	0.7	adom	6	A4	140m	18m N
851	0.7	adom	7	A4	160m	22m N
851	0.7	adom	8	A4	200m	18m N
851	0.7	adom	9	*	lg ellipse	23m @ 18deg
851	0.7	adom	10	*	lg ellipse	8m @ 198deg
851	0.7	adom	11	*	sm ellipse	17m @ 18deg
851	0.7	adom	12	*	sm ellipse	12m @198deg
854	0.2	adom	1	A4	40m	28m S
854	0.2	adom	2	A4	80m	22m N
854	0.2	adom	3	A4	80m	20m S
854	0.2	adom	4	A4	100m	19m N
854	0.2	adom	5	A4	100m	21m S
854	0.2	adom	6	A4	140m	23m N
854	0.2	adom	7	A4	160m	20m S
854	0.2	adom	8	A4	180m	22m S
854	0.2	adom	9	*	lg ellipse	8m @ 18deg
854	0.2	adom	10	*	lg ellipse	8m @ 198deg
854	0.2	adom	11	*	sm ellipse	13m @18deg
854	0.2	adom	12	*	sm ellipse	3m @198deg
857	m burn	adom	1	A1	80m	30m W
857	m burn	adom	2	A1	100m	8m W
857	m burn	adom	3	A1	160m	25m W
857	m burn	adom	4	A1	160m	9m E
857	m burn	adom	5	A1	180m	17m W
857	m burn	adom	6	A1	180m	22m E
857	m burn	adom	7	A1	200m	13m E
857	m burn	adom	8	A1	240m	27m E

858	h burn	adom	1	A1	80m	8m W
858	h burn	adom	2	A1	80m	14m E
858	h burn	adom	3	A1	100m	8m E
858	h burn	adom	4	A2	40m	9m S
858	h burn	adom	5	A2	60m	17m N
858	h burn	adom	6	A2	60m	26m S
858	h burn	adom	7	A2	80m	18m N
858	h burn	adom	8	A2	80m	19m S
859	0.7	adom	1	A1	20m	9m W
859	0.7	adom	2	A1	60m	6m E
859	0.7	adom	3	A1	60m	15m E
859	0.7	adom	4	A1	60m	1m E
859	0.7	adom	5	A1	80m	16m E
859	0.7	adom	6	A1	120m	20m E
859	0.7	adom	7	A1	140m	15m E
859	0.7	adom	8	A1	160m	10m E
859	0.7	adom	9	*	lg ellipse	15m @ 25deg
859	0.7	adom	10	*	lg ellipse	24m @ 205deg
859	0.7	adom	11	*	sm ellipse	10m @ 25deg
859	0.7	adom	12	*	sm ellipse	1m @ 205deg
860	0.2	adom	1	B3	60m	8m N
860	0.2	adom	2	B3	80m	24m N
860	0.2	adom	3	B3	100m	16m N
860	0.2	adom	4	B3	160m	13m N
860	0.2	adom	5	B3	180m	6m S
860	0.2	adom	6	B3	200m	9m S
860	0.2	adom	7	B3	220m	4m S
860	0.2	adom	8	B3	240m	6m S
860	0.2	adom	9	*	lg ellipse	15m @ 25deg
860	0.2	adom	10	*	lg ellipse	18m @ 205deg
860	0.2	adom	11	*	sm ellipse	13m @ 25deg
860	0.2	adom	12	*	sm ellipse	23m @ 205deg
864	clearcut	adom	1	B2	20m	6m N
864	clearcut	adom	2	B2	20m	23m N
864	clearcut	adom	3	B2	60m	8m N
864	clearcut	adom	4	B2	80m	16m N
864	clearcut	adom	5	B2	120m	5m N
864	clearcut	adom	6	B2	140m	2m N
864	clearcut	adom	7	B2	140m	25m N
864	clearcut	adom	8	B2	160m	4m N
865	m burn	adom	1	B2	80m	3m S
865	m burn	adom	2	B2	100m	4m S
865	m burn	adom	3	B2	120m	13m N
865	m burn	adom	4	B2	120m	11m S
865	m burn	adom	5	B2	140m	7m N
865	m burn	adom	6	B2	160m	23m N
865	m burn	adom	7	B2	180m	10m N
865	m burn	adom	8	B2	180m	1m S

872	m burn	mix	1	E2	20m	3m N
872	m burn	mix	2	E2	40m	13m N
872	m burn	mix	3	E3	20m	3m N
872	m burn	mix	4	E3	60m	24m S
872	m burn	mix	5	E3	80m	1m S
872	m burn	mix	6	E3	100m	9m N
872	m burn	mix	7	E3	100m	24m S
872	m burn	mix	8	E3	140m	15m S
874	clearcut	mix	1	E7	60m	16m N
874	clearcut	mix	2	E7	160m	8m N
874	clearcut	mix	3	E7	180m	25m N
874	clearcut	mix	4	E7	220m	20m S
874	clearcut	mix	5	E7	240m	12m N
874	clearcut	mix	6	E7	240m	8m S
874	clearcut	mix	7	E7	260m	9m N
874	clearcut	mix	8	E7	280m	10m N
875	0.2	mix	1	E2	80m	19m W
875	0.2	mix	2	E2	80m	18m E
875	0.2	mix	3	E2	100m	20m W
875	0.2	mix	4	E2	120m	10m E
875	0.2	mix	5	E2	140m	19m W
875	0.2	mix	6	E2	140m	15m E
875	0.2	mix	7	E2	160m	10m W
875	0.2	mix	8	E2	160m	11m E
875	0.2	mix	9	*	lg ellipse	24m N
875	0.2	mix	10	*	lg ellipse	28m S
875	0.2	mix	11	*	sm ellipse	18m N
875	0.2	mix	12	*	sm ellipse	14m S
890	0.7	cdom	1	D2	20m	14m N
890	0.7	cdom	2	D2	20m	11m S
890	0.7	cdom	3	D2	40m	20m S
890	0.7	cdom	4	D2	60m	4m N
890	0.7	cdom	5	D2	60m	10m S
890	0.7	cdom	6	D2	120m	9m N
890	0.7	cdom	7	D2	140m	30m N
890	0.7	cdom	8	D2	160m	21m N
890	0.7	cdom	9	*	lg ellipse	24m N
890	0.7	cdom	10	*	lg ellipse	8m S
890	0.7	cdom	11	*	sm ellipse	16m N
890	0.7	cdom	12	*	sm ellipse	9m S
892	clearcut	cdom	1	D2	80m	8m S
892	clearcut	cdom	2	D2	100m	28m S
892	clearcut	cdom	3	D2	120m	15m S
892	clearcut	cdom	4	D2	160m	28m N
892	clearcut	cdom	5	D2	220m	5m N
892	clearcut	cdom	6	D2	240m	18m N
892	clearcut	cdom	7	D2	260m	22m S
892	clearcut	cdom	8	D2	300m	1m N

896	0.2	cdom	1	D7	80m	7m S
896	0.2	cdom	2	D7	80m	7m S*
896	0.2	cdom	3	D7	100m	12m N
896	0.2	cdom	4	D7	100n	1m S
896	0.2	cdom	5	D7	120m	12m N
896	0.2	cdom	6	D7	120m	8m S
896	0.2	cdom	7	D7	140m	22m N
896	0.2	cdom	8	D7	160m	2m S
896	0.2	cdom	9	*	lg ellipse	13m N
896	0.2	cdom	10	*	lg ellipse	16m S
896	0.2	cdom	11	*	sm ellipse	6m N
896	0.2	cdom	12	*	sm ellipse	24m S
897	m burn	cdom	1	D10	40m	11m E
897	m burn	cdom	2	D10	60m	18m W
897	m burn	cdom	3	D10	60m	18m E
897	m burn	cdom	4	D10	80m	10m W
897	m burn	cdom	5	D10	80m	7m E
897	m burn	cdom	· 6	D10	160m	3m W
897	m burn	cdom	7	D10	180m	4m W
897	m burn	cdom	8	D10	180m	13m E
899	clearcut	mix	1	D9	40m	19m N
899	clearcut	mix	2	D9	40m	5m S
899	clearcut	mix	3	D9	80m	23m N
899	clearcut	mix	4	D9	80m	13m S
899	clearcut	mix	5	D9	100m	23m N
899	clearcut	mix	6	D9	100m	6m S
899	clearcut	mix	7	D9	160m	8m N
899	clearcut	mix	8	D9	160m	1m S
901	m burn	mix	1	D9	100m	3m S
901	m burn	mix	2	D9	180m	29m N
901	m burn	mix	3	D9	200m	3m N
901	m burn	mix	4	D9	200m	14m S
901	m burn	mix	5	D9	220m	1m N
901	m burn	mix	6	D9	240m	9m N
901	m burn	mix	7	D9	240m	24m S
901	m burn	mix	8	D9	260m	13m S
905	0.2	mix	1	H1	80m	12m N
905	0.2	mix	2	H1	80m	2m S
905	0.2	mix	3	H1	100m	11m N
905	0.2	mix	4	H1	100m	28m S
905	0.2	mix	5	H1	140m	7m N
905	0.2	mix	6	H1	140m	20m S
905	0.2	mix	7	H1	160m	6m N
905	0.2	mix	8	H1	160m	19m S
905	0.2	mix	9	*	lg ellipse	14m N
905	0.2	mix	10	*	lg ellipse	1m S
905	0.2	mix	11	*	sm ellipse	1m N
905	0.2	mix	12	*	sm ellipse	15m S

906	0.7	mix	1	H1	20m	20m E
906	0.7	mix	2	H1	40m	17m W
906	0.7	mix	3	H1	40m	21m E
906	0.7	mix	4	H1	60m	10m W
906	0.7	mix	5	H1	60m	11m E
906	0.7	mix	6	H1	80m	9m W
906	0.7	mix	7	H1	80m	27m E
906	0.7	mix	8	H1	100m	21m W
906	0.7	mix	9	*	lg ellipse	8m N
906	0.7	mix	10	*	lg ellipse	2m S
906	0.7	mix	11	*	sm ellipse	1m N
906	0.7	mix	12	*	sm ellipse	19m S
907	0.7	adom	1	F1	40m	18m W
907	0.7	adom	2	F1	40m	9m E
907	0.7	adom	3	F1	60m	6m W
907	0.7	adom	4	F1	80m	3m W
907	0.7	adom	5	F1	80m	17m E
907	0.7	adom	6	F1	100m	23m E
907	0.7	adom	7	F1	140m	2m E
907	0.7	adom	8	F1	220m	25m E
907	0.7	adom	9	*	lg ellipse	19m N
907	0.7	adom	10	*	lg ellipse	1m S
907	0.7	adom	11	*	sm ellipse	8m N
907	0.7	adom	12	*	sm ellipse	3m S
909	0.7	mix	1	G2	60m	14m W
909	0.7	mix	2	G2	60m	23m E
909	0.7	mix	3	G2	80m	24m E
909	0.7	mix	4	G3	40m	15m W
909	0.7	mix	5	G3	60m	22m W
909	0.7	mix	6	G3	60m	2m E
909	0.7	mix	7	G3	80m	11m E
909	0.7	mix	8	G3	100m	9m W
909	0.7	mix	9	*	lg ellipse	14m N
909	0.7	mix	10	*	lg ellipse	26m S
909	0.7	mix	11	*	sm ellipse	5m N
909	0.7	mix	12	*	sm ellipse	4m S
910	0.2	mix	1	I2	100m	14m N
910	0.2	mix	2	I2	100m	3m S
910	0.2	mix	3	I2	120m	13m S
910	0.2	mix	4	I2	140m	29m N
910	0.2	mix	5	I2	140m	1m S
910	0.2	mix	6	I2	160m	9m N
910	0.2	mix	7	I2	160m	29m S
910	0.2	mix	8	I2	180m	29m N
910	0.2	mix	9	*	lg ellipse	7m N
910	0.2	mix	10	*	lg ellipse	24m S
910	0.2	mix	11	*	sm ellipse	25m N
910	0.2	mix	12	*	sm ellipse	13m S

912	0.7	mix	1	I3	120m	23m N
912	0.7	mix	2	I3	120m	30m S
912	0.7	mix	3	I3	140m	11m N
912	0.7	mix	4	I3	180m	13m N
912	0.7	mix	5	I3	200m	4m N
912	0.7	mix	6	I3	200m	18m S
912	0.7	mix	7	I3	240m	3m S
912	0.7	mix	8	I3	260m	28m N
912	0.7	mix	9	*	lg ellipse	7m N
912	0.7	mix	10	*	lg ellipse	1m S
912	0.7	mix	11	*	sm ellipse	11m N
912	0.7	mix	12	*	sm ellipse	10m S
914	clearcut	mix	1	I4	40m	29m S
914	clearcut	mix	2	I4	60m	5m N
914	clearcut	mix	3	I4	60m	18m S
914	clearcut	mix	4	I4	120m	19m N
914	clearcut	mix	5	I4	160m	17m N
914	clearcut	mix	6	I4	160m	21m S
914	clearcut	mix	7	I4	180m	16m N
914	clearcut	mix	8	I4	180m	15m S
916	m burn	cdom	1	J2	80m	23m N
916	m burn	cdom	2	J2	120m	15m N
916	m burn	cdom	3	J2	120m	15m S
916	m burn	cdom	4	J2	140m	7m N
916	m burn	cdom	5	J2	140m	11m S
916	m burn	cdom	6	J2	160m	22m N
916	m burn	cdom	7	J2	160m	2m S
916	m burn	cdom	8	J2	200m	10m N
919	0.2	cdom	1	J1	360m	3m W
919	0.2	cdom	2	J1	400m	11m W
919	0.2	cdom	3	J1	420m	19m E
919	0.2	cdom	4	J1	460m	9m W
919	0.2	cdom	5	J1	460m	14m E
919	0.2	cdom	6	J1	500m	12m W
919	0.2	cdom	7	J1	500m	27m E
919	0.2	cdom	8	J1	520m	23m W
919	0.2	cdom	9	*	lg ellipse	6m N
919	0.2	cdom	10	*	lg ellipse	19m S
919	0.2	cdom	11	*	sm ellipse	13m N
919	0.2	cdom	12	*	sm ellipse	9m S

921	0.7	cdom	1	J5	20m	11m N
921	0.7	cdom	2	J5	20m	19m S
921	0.7	cdom	3	J5	60m	13m N
921	0.7	cdom	4	J5	60m	22m S
921	0.7	cdom	5	J5	140m	14m S
921	0.7	cdom	6	J5	160m	7m N
921	0.7	cdom	7	J5	200m	30m N
921	0.7	cdom	8	J5	220m	10m N
921	0.7	cdom	9	*	lg ellipse	25m N
921	0.7	cdom	10	*	lg ellipse	7m S
921	0.7	cdom	11	*	sm ellipse	10 m N
921	0.7	cdom	12	*	sm ellipse	2m S
922	clearcut	cdom	1	J3	40m	4m E
922	clearcut	cdom	2	J3	60m	14m W
922	clearcut	cdom	3	J3	60m	7m E
922	clearcut	cdom	4	J3	60m	25m E
922	clearcut	cdom	5	J3	140m	7m W
922	clearcut	cdom	6	J3	160m	6m W
922	clearcut	cdom	7	J3	160m	8m E
922	clearcut	cdom	8	J3	200m	15m W
923	h burn	cdom	1	J3	60m	25m E
923	h burn	cdom	2	J3	80m	22m W
923	h burn	cdom	3	J3	80m	21m E
923	h burn	cdom	4	J3	100m	4m W
923	h burn	cdom	5	J3	100m	4m E
923	h burn	cdom	6	J3	120m	9m W
923	h burn	cdom	7	J3	120m	13m E
923	h burn	cdom	8	J3	140m	17m W
926	m burn	cdom	1	K1	60m	26m W
926	m burn	cdom	2	K2	80m	9m W
926	m burn	cdom	3	K2	80m	17m E
926	m burn	cdom	4	K2	100m	27m W
926	m burn	cdom	5	K2	100m	25m E
926	m burn	cdom	6	K2	120m	13m W
926	m burn	cdom	7	K2	120m	14m E
926	m burn	cdom	8	K2	140m	8m W
931	0.7	cdom	1	L1	20m	13m S
931	0.7	cdom	2	L1	40m	19m S
931	0.7	cdom	3	L1	60m	9m S
931	0.7	cdom	4	L1	100m	18m S
931	0.7	cdom	5	L1	120m	5m N
931	0.7	cdom	6	L1	120m	23m S
931	0.7	cdom	7	L1	140m	7m N
931	0.7	cdom	8	L1	140m	27m S
931	0.7	cdom	9	*	lg ellipse	12m N
931	0.7	cdom	10	*	lg ellipse	15m S
931	0.7	cdom	11	*	sm ellipse	7m N
931	0.7	cdom	12	*	sm ellipse	4m S

932	clearcut	cdom	1	L2	60m	10m N
932	clearcut	cdom	2	L2	60m	12m S
932	clearcut	cdom	3	L2	120m	21m N
932	clearcut	cdom	4	L2	160m	17m S
932	clearcut	cdom	5	L2	180m	23m S
932	clearcut	cdom	6	L2	340m	22m S
932	clearcut	cdom	7	L2	360m	4m S
932	clearcut	cdom	8	L2	380m	16m S
933	0.2	cdom	1	L1	60m	2m N
933	0.2	cdom	2	L1	60m	15m S
933	0.2	cdom	3	L1	80m	8m N
933	0.2	cdom	4	L1	80m	7m S
933	0.2	cdom	5	L1	100m	16m N
933	0.2	cdom	6	L1	100m	5m S
933	0.2	cdom	7	L1	120m	11m N
933	0.2	cdom	8	L1	120m	27m S
933	0.2	cdom	9	*	lg ellipse	22m N
933	0.2	cdom	10	*	lg ellipse	14m S
933	0.2	cdom	11	*	sm ellipse	13m N
933	0.2	cdom	12	*	sm ellipse	1m S
937	h burn	mix	1	M2	60m	13m S
937	h burn	mix	2	M2	80m	25m S
937	h burn	mix	3	M2	100m	4m N
937	h burn	mix	4	M2	140m	7m N
937	h burn	mix	5	M2	160m	24m S
937	h burn	mix	6	M2	180m	29m S
937	h burn	mix	7	M2	200m	29m N
937	h burn	mix	8	M2	220m	1m N
938	m burn	mix	1	M1	100m	10m N
938	m burn	mix	2	M1	140m	16m N
938	m burn	mix	3	M1	160m	3m N
938	m burn	mix	4	M1	180m	13m N
938	m burn	mix	5	M1a	80m	3m S
938	m burn	mix	6	M1a	160m	8m S
938	m burn	mix	7	M1a	180m	11m S
938	m burn	mix	8	M1a	200m	29m S
941	clearcut	adom	1	N7	60m	23m W
941	clearcut	adom	2	N7	80m	19m W
941	clearcut	adom	3	N7	100m	10m W
941	clearcut	adom	4	N7	120m	16m W
941	clearcut	adom	5	N7	160m	18m W
941	clearcut	adom	6	N7	200m	26m W
941	clearcut	adom	7	N7	260m	7m E
941	clearcut	adom	8	N7	340m	13m E

942	m burn	adom	1	N3	80m	17m E
942	m burn	adom	2	N3	100m	21m E
942	m burn	adom	3	N3	120m	4m E
942	m burn	adom	4	N3	160m	11m E
942	m burn	adom	5	N3	200m	25m E
942	m burn	adom	6	N3	220m	22m E
942	m burn	adom	7	N3	240m	4m E
942	m burn	adom	8	N3	300m	3m W
952	0.2	adom	1	P2	20m	19m W
952	0.2	adom	2	P2	20m	20m E
952	0.2	adom	3	P2	40m	12m W
952	0.2	adom	4	P2	60m	8m W
952	0.2	adom	5	P3	20m	13m S
952	0.2	adom	6	P3	40m	9m S
952	0.2	adom	7	P3	60m	19m S
952	0.2	adom	8	P3	80m	7m S
952	0.2	adom	9	*	lg ellipse	9m N
952	0.2	adom	10	*	lg ellipse	19m S
952	0.2	adom	11	*	sm ellipse	7m N
952	0.2	adom	12	*	sm ellipse	20m S

* all plots in ellipses located in relation to ellipse center

Appendix 2. *Classification systems*

Cover classes

1	<1%
2	1-3%
3	4-10%
4	11-25%
5	26-50%
6	51-75%
7	>75%

Litter type classes

1	v.fine - leaf/needle litter
2	
3	fine - small twigs, chipped wood
4	
5	coarse - small branches <5cm diam
6	
7	v. coarse - large branches >5 and <8cm diam

Corridor classes

1	0-19% of shrub plot in machine corridor
2	20-39% of shrub plot in machine corridor
3	40-59% of shrub plot in machine corridor
4	60-79% of shrub plot in machine corridor
5	80-100% of shrub plot in machine corridor

Decay classes

1	undecayed, hard includes branches
2	hard, no twigs, >50% bark
3	<50% bark, soft spots
4	no bark, soft, fungi and mosses
5	large pieces missing, deformed, moss
6	decayed, mosses and vascular plants
7	well decayed, vague outline

Appendix 3. Species List

	Species	abbreviation	common name
Herbs &	*Achillea millefolium*	acmi	yarrow
Dwarf	*Actea rubra*	acru	baneberry
Shrubs	*Anemone parviflora*	anpa	
	Aralia nudicaulus	arnu	wild sarsparilla
	Aster spp.	assp	aster
	Astragalus americanus	asam	American milk vetch
	Bromus spp.	brsp	brome grass
	Calamagrostis canadensis	caca	bluejoint
	Carex spp.	casp	sedges
	Circea alpina	cial	enchanter's nightshade
	Corallorhiza trifida	cotr	pale coralroot
	Cornus canadensis	coca	bunchberry
	Corydalis aurea	coau	golden corydalis
	Delphinium glaucum	degl	tall larkspur
	Dryopteris austriaca	drau	wood fern
	Elymus innovatum	elin	hairy wild rye
	Epilobium angustifolium	epan	fireweed
	Equisetum arvense	eqar	common horsetail
	Equisetum fluviatile	eqfl	swamp horsetail
	Equisetum scirpoides	eqsc	
	Equisetum sylvaticum	eqsy	woodland horsetail
	Fragaria vesca	frve	woodland strawberry
	Fragaria virginiana	frvi	wild strawberry
	Galium boreale	gabo	northern bedstraw
	Galium triflorum	gatr	sweet-scented bedstraw
	Geocaulon lividum	geli	bastard toadflax
	Geum macrophyllum	gema	yellow avens
	Goodyeara repens	gore	rattlesnake plantain
	Habeneria obtusata	haob	blunt-leaved orchid
	Habeneria orbiculata	haor	round-leaved orchid
	Halenia deflexa	hade	spurred gentian
	Heracleum lanatum	hela	cow parsnip
	Lathyrus spp.	lasp	peavine sp.
	Linnaea borealis	libo	twinflower
	Lycopodium annotatum	lyan	ground cedar
	Lycopodium complanatum	lyco	stiff club-moss
	Maianthemum canadense	maca	wild lily of the valley
	Mertensia paniculata	mepa	tall lungwort/bluebells
	Mitella nuda	minu	bishop's cap
	Mitella pentandra	mipe	
	Moneses uniflora	moun	one-flowered wintergreen
	Osmorhiza depauperata	osde	sweet-spreading cicely
	Pediculara labradorica	pela	labrador lousewort
	Petasites frigidus	pefr	arctic coltsfoot
	Petasites palmatus	pepa	palmate-leaved coltsfoot
	Petasites saggitus	pesa	arrow-leaved coltsfoot
	Poa palustris	popa	fowl bluegrass

Poa pratensis	popr	Kentucky bluegrass
Pyrola asarafolia	pyas	common pink wintergreen
Pyrola secunda	pyse	one-sided wintergreen
Pyrola virens	pyvi	green wintergreen
Rubus acaulis	ruac	dwarf raspberry
Rubus pubescens	rupu	dewberry
Thalictrum venulosum	thve	veiny meadow rue
Trientalis boreale	trbo	northern starflower
Vaccinium caespitosum	vaca	dwarf blueberry
Vaccinium vitis-idea	vavi	bog cranberry
Vicea americana	viam	wild vetch
Viola canadensis	vica	western Canada violet
Viola renifolia	vire	kidney-leaved violet

Shrubs & Trees	*Alnus spp.*	alsp	alder
	Amelanchier alnifolia	amal	saskatoon
	Betula glandulosum	begl	dwarf birch
	Betula papyrifera	bepa	paper birch
	Cornus stolonifera	cost	red-osier dogwood
	Ledum groenlandicum	legr	labrador tea
	Lonicera dioica	lodi	bracted honeysuckle
	Picea glauca	pigl	white spruce
	Populus balsamifera	poba	balsam poplar
	Populus tremuloides	potr	trembling aspen
	Ribes americana	riam	wild black currant
	Ribes glandulosum	rigl	skunk currant
	Ribes hudsonianum	rihu	wild black currant
	Ribes lacustre	rila	bristly black currant
	Ribes oxyacanthoides	riox	northern gooseberry
	Ribes triste	ritr	red swamp currant
	Rosa acicularis	roac	prickly rose
	Rubus idaeus	ruid	wild red raspberry
	Salix spp.	sasp	willow sp.
	Sheperdia canadensis	shca	buffaloberry
	Sorbus scopulina	sosc	mountain ash
	Symphorocarpus occidentalis	symp	western snowberry
	Viburnum edule	vied	lobush cranberry

Appendix 4. Species Presence/Absence Table

Standtype	Deciduous dominated											
Treatment	clearcut			20%			75%			control		
Harvest Year	pre	post 1	post 2	pre	post 1	post 2	pre	post 1	post 2	pre	post 1	post 2
Achi mil	●	●	●	●	●	●	●	●	●	●	●	●
Alnus sp.	●	●	●	●	●	●	●	●	●	●	●	●
Aster sp.	●	●	●	●	●	●	●	●	●	●	●	●
Cala can	●	●	●	●	●	●	●	●	●	●	●	●
Corn can	●	●	●	●	●	●	●	●	●	●	●	●
Elym inn	●	●	●	●	●	●	●	●	●	●	●	●
Epil ang	●	●	●	●	●	●	●	●	●	●	●	●
Equi arv	●	●	●	●	●	●	●	●	●	●	●	●
Frag vir	●	●	●	●	●	●	●	●	●	●	●	●
Gali bor	●	●	●	●	●	●	●	●	●	●	●	●
Gali triflor	●	●	●	●	●	●	●	●	●	●	●	●
Lathy sp.	●	●	●	●	●	●	●	●	●	●	●	●
Linn bor	●	●	●	●	●	●	●	●	●	●	●	●
Maia can	●	●	●	●	●	●	●	●	●	●	●	●
Mert pan	●	●	●	●	●	●	●	●	●	●	●	●
Mite nud	●	●	●	●	●	●	●	●	●	●	●	●
Popu tre	●	●	●	●	●	●	●	●	●	●	●	●
Pyro asa	●	●	●	●	●	●	●	●	●	●	●	●
Ribe oxy	●	●	●	●	●	●	●	●	●	●	●	●
Ribe tri	●	●	●	●	●	●	●	●	●	●	●	●
Rosa aci	●	●	●	●	●	●	●	●	●	●	●	●
Rubu pub	●	●	●	●	●	●	●	●	●	●	●	●
Shep can	●	●	●	●	●	●	●	●	●	●	●	●
Vibu edu	●	●	●	●	●	●	●	●	●	●	●	●
Vici ame	●	●	●	●	●	●	●	●	●	●	●	●
Viol ren	●	●	●	●	●	●	●	●	●	●	●	●
Acta rub	●	●	●		●	●	●	●	●	●	●	●
Amel aln										●		
Aral nud	●						●	●	●	●	●	●
Astr ame	●		●	●	●	●				●	●	●
Betu gla	●		●					●		●		●
Corn sto		●						●		●		●
Delp gla		●	●	●	●	●	●	●	●	●	●	●
Equi flu		●										
Equi sci											●	
Equi syl	●	●	●	●	●	●	●		●	●		
Frag ves	●	●						●		●		
Geoc liv									●			
Habe obt	●											
Hale def										●	●	

131

	1	2	3	4	5	6	7	8	9	10	11	12
Hera lan	•	•	•					•	•	•	•	•
Ledu gro		•			•							
Loni dio	•						•		•	•	•	•
Lyco ann							•	•	•			
Lyco com	•	•	•									
Mite pen				•								
Osmo dep	•			•	•	•	•	•	•	•	•	•
Peta fri	•			•			•			•	•	
Peta pal	•			•			•			•		
Peta sag		•	•		•	•		•	•		•	•
Pice gla	•	•		•	•			•		•	•	•
Poa pal		•			•			•				
Poa pra	•				•					•	•	
Popu bal	•	•	•	•	•	•	•		•	•	•	
Pyro sec	•	•	•	•	•	•	•	•	•		•	
Pyro vir								•				
Ribe gla		•						•			•	
Ribe hud							•					
Ribe lac							•		•	•	•	
Rubu ida	•	•	•	•	•	•	•	•	•	•	•	
Salix sp.				•			•				•	
Symph				•		•				•	•	•
Thal ven	•		•		•							
Vacc cae	•	•	•			•		•		•	•	•
Vacc vit		•			•			•			•	
Viol can		•		•	•		•	•	•	•	•	•
Anem par												
Betu pap												
Bromus sp.												
Care dis												
Care ten												
Circ alp												
Cora tri												
Cory aur												
Dryo aus												
Geum mac												
Good rep												
Habe orb												
Hypo phy												
Mone uni												
Oxyc mic												
Pedi lab												
Ribe ame												
Rubu aca												
Sorb sco												
Trie bor												

Standtype	Conifer dominated											
Treatment	clearcut			20%			75%			control		
Harvest Year	pre	post 1	post 2	pre	post 1	post 2	pre	post 1	post 2	pre	post 1	post 2
Alnus sp.	●	●	●	●	●	●	●	●	●	●	●	●
Corn can	●	●	●	●	●	●	●	●	●	●	●	●
Elym inn	●	●	●	●	●	●	●	●	●	●	●	●
Epil ang	●	●	●	●	●	●	●	●	●	●	●	●
Equi arv	●	●	●	●	●	●	●	●	●	●	●	●
Equi syl	●	●	●	●	●	●	●	●	●	●	●	●
Frag vir	●	●	●	●	●	●	●	●	●	●	●	●
Gali bor	●	●	●	●	●	●	●	●	●	●	●	●
Lathy sp.	●	●	●	●	●	●	●	●	●	●	●	●
Linn bor	●	●	●	●	●	●	●	●	●	●	●	●
Mert pan	●	●	●	●	●	●	●	●	●	●	●	●
Mite nud	●	●	●	●	●	●	●	●	●	●	●	●
Ribe tri	●	●	●	●	●	●	●	●	●	●	●	●
Rosa aci	●	●	●	●	●	●	●	●	●	●	●	●
Rubu pub	●	●	●	●	●	●	●	●	●	●	●	●
Vibu edu	●	●	●	●	●	●	●	●	●	●	●	●
Viol ren	●	●	●	●	●	●	●	●	●	●	●	●
Achi mil			●		●	●						
Acta rub												●
Anem par								●				
Aral nud				●	●	●	●	●	●	●		●
Aster sp.	●	●	●		●	●		●		●	●	●
Astr ame											●	
Betu gla							●					
Cala can	●		●	●	●	●	●	●	●	●	●	●
Circ alp				●			●	●	●	●		●
Cory aur			●									
Delp gla	●			●	●	●	●	●	●	●		
Equi flu					●							
Equi sci	●											
Gali triflor	●		●	●	●	●	●	●	●	●	●	●
Geoc liv	●											
Geum mac								●				
Good rep	●			●			●					
Habe obt							●					
Habe orb							●					
Hera lan							●	●	●			
Ledu gro	●	●				●	●		●			
Loni dio								●				
Lyco ann	●	●					●	●	●	●	●	●
Maia can	●	●	●	●	●	●		●				

	1	2	3	4	5	6	7	8	9	10	11	12
Mone uni				●			●					
Osmo dep							●					
Peta fri				●							●	
Peta pal	●			●			●			●		
Peta sag		●	●		●	●		●	●		●	●
Pice gla			●					●			●	
Poa pal							●					
Poa pra					●							
Popu bal	●	●	●			●	●	●	●	●	●	
Popu tre	●	●	●	●	●	●	●	●	●		●	●
Pyro asa	●		●	●	●	●	●	●		●		●
Pyro sec	●	●		●			●	●		●	●	
Pyro vir	●			●			●					
Ribe ame							●					
Ribe gla				●							●	
Ribe hud							●					
Ribe lac					●	●		●		●	●	●
Ribe oxy	●	●	●		●		●	●	●		●	
Rubu aca					●							
Rubu ida	●	●		●	●	●	●	●	●	●	●	●
Salix sp.	●	●			●							
Shep can		●		●	●	●	●	●	●	●	●	●
Thal ven									●			
Trie bor					●							
Vacc cae	●		●	●		●	●	●	●		●	
Vacc vit	●	●		●	●		●	●	●	●	●	●
Vici ame		●						●				
Viol can	●	●		●	●		●	●			●	
Amel aln												
Betu pap												
Bromus sp.												
Care dis												
Care ten												
Cora tri												
Corn sto												
Dryo aus												
Frag ves												
Hale def												
Hypo phy												
Lyco com												
Mite pen												
Oxyc mic												
Pedi lab												
Sorb sco												
Symph												

| Standtype	Mixedwood											
Treatment	clearcut			20%			75%			control		
Harvest Year	pre	post 1	post 2	pre	post 1	post 2	pre	post 1	post 2	pre	post 2	post 1
Aster sp.	●	●	●	●	●	●	●	●	●	●	●	●
Corn can	●	●	●	●	●	●	●	●	●	●	●	●
Elym inn	●	●	●	●	●	●	●	●	●	●	●	●
Epil ang	●	●	●	●	●	●	●	●	●	●	●	●
Equi syl	●	●	●	●	●	●	●	●	●	●	●	●
Frag vir	●	●	●	●	●	●	●	●	●	●	●	●
Lathy sp.	●	●	●	●	●	●	●	●	●	●	●	●
Linn bor	●	●	●	●	●	●	●	●	●	●	●	●
Mert pan	●	●	●	●	●	●	●	●	●	●	●	●
Mite nud	●	●	●	●	●	●	●	●	●	●	●	●
Popu tre	●	●	●	●	●	●	●	●	●	●	●	●
Pyro sec	●	●	●	●	●	●	●	●	●	●	●	●
Ribe tri	●	●	●	●	●	●	●	●	●	●	●	●
Rosa aci	●	●	●	●	●	●	●	●	●	●	●	●
Rubu pub	●	●	●	●	●	●	●	●	●	●	●	●
Shep can	●	●	●	●	●	●	●	●	●	●	●	●
Vibu edu	●	●	●	●	●	●	●	●	●	●	●	●
Viol ren	●	●	●	●	●	●	●	●	●	●	●	●
Achi mil	●			●	●	●						
Acta rub					●	●	●	●	●			●
Alnus sp.	●	●	●	●	●		●	●	●	●	●	●
Anem par											●	
Aral nud	●	●	●							●	●	●
Astr ame	●						●			●	●	●
Betu pap	●		●							●		
Bromus sp.						●						
Cala can	●	●	●			●	●	●	●	●	●	●
Care dis	●									●		
Care ten	●											
Circ alp									●			
Cora tri							●					
Cory aur						●						
Delp gla					●		●	●	●	●	●	●
Dryo aus	●						●	●	●			
Equi arv	●		●	●	●	●	●	●	●	●	●	●
Equi sci	●									●		
Frag ves					●							●
Gali bor		●		●			●	●		●	●	●
Gali triflor	●	●	●		●	●	●	●	●	●	●	●
Geoc liv	●			●								
Good rep				●	●		●			●		●

	1	2	3	4	5	6	7	8	9	10	11	12
Habe obt	•			•						•	•	•
Habe orb				•	•					•		
Hera lan		•										
Hypo phy							•					
Ledu gro				•						•	•	•
Loni dio			•							•	•	•
Lyco ann	•	•		•			•	•	•	•	•	•
Lyco com				•	•	•	•	•	•			
Maia can	•	•		•	•	•	•	•	•	•	•	•
Mone uni	•			•						•		
Osmo dep				•				•	•			
Pedi lab	•											
Peta fri	•						•			•	•	•
Peta pal	•		•	•			•			•		
Peta sag		•	•		•	•		•	•		•	•
Pice gla	•					•	•		•	•	•	•
Poa pal												•
Poa pra										•		
Popu bal		•	•		•	•		•	•	•	•	•
Pyro asa	•		•	•	•	•	•	•	•	•	•	•
Pyro vir				•			•					
Ribe gla										•	•	
Ribe lac	•			•			•		•	•		•
Ribe oxy		•			•			•		•	•	•
Rubu aca		•						•				
Rubu ida	•	•	•		•			•	•	•	•	•
Salix sp.	•			•				•		•		•
Sorb sco	•											
Vacc cae	•	•		•		•	•	•	•	•		•
Vacc vit	•	•		•	•	•	•	•	•	•	•	•
Vici ame		•	•		•							
Viol can	•				•		•	•				•
Amel aln												
Betu gla												
Corn sto												
Equi flu												
Geum mac												
Hale def												
Mite pen												
Oxyc mic												
Ribe ame												
Ribe hud												
Symph												
Thal ven												
Trie bor												

Appendix 5. Stand descriptions

Forest type	Range of mean age/stand (years)	Stand # Replicate	Stand # EMEND	Compartments	AVI Description
DD		1	77	850, 851, 854, 857, 858	C25Aw9Pb1-90-G
	70.1 - 93.4 deciduous species	2	66	859, 860, 864, 865	C25Aw9Pb1-90-G
		3	121	907	C24Aw8Pb1Sw1-90-G
			9481	941, 942	C23Aw9Pb1-90-M
			582	952	C24Aw10-f-89-M
MX	58.3 – 125.9 deciduous species	7	49	872, 874, 875	C22Aw7Sw2Pb1-89-M
			254	909	B23Aw6Sw4-89-M
		8	29	899, 901	C26Sw6Aw4-88-G
			202	905, 906	C26Sw7Aw3-89-G
	85.0 – 131.6 coniferous species	9	303	910, 912, 914	C26Sw7Aw2Fb1-89-G
		.	423	937, 938	C26Sw6Aw4-89-G
CD		4	31	890, 892, 896, 897	B30Sw10-88-G
	113.9-147.0 conifer species	5	314	916, 919, 921, 922, 923	C26Sw9Aw1-89-G
		6	306	926	B28Sw8Aw2-88-G
			446	931, 932, 933	C23Sw9Aw1-90-G

Key to AVI codes

Crown closure ——— C 25 Aw9Pb1 -90- G ——— Site quality

crown height

Species type and cover

Year of establishment 1**0
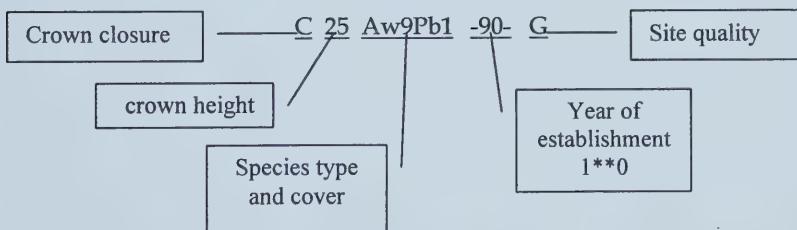
Crown closure	
Code	%
A	06-30
B	31-50
C	51-70
D	71-100

Site quality	
Code	Explantion
G	Good
M	Medium

Tree species	
Code	Name
Aw	Populus tremuloides
Fb	Abies balsamifera
Sw	Picea glauca
Pb	Populus balsamifera